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# PARASITOLOGY

EDITED BY

GEORGE H. F. NUTTALL, M.D., Ph.D., Sc.D., F.R.S.

Quick Professor of Biology and Director of the Molteno Institute for Research in Parasitology in the University of Cambridge

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VOLUME XIV JUNE, 1922 No. 2

# THE MOLTENO INSTITUTE FOR RESEARCH IN PARASITOLOGY, UNIVERSITY OF CAMBRIDGE, WITH AN ACCOUNT OF HOW IT CAME TO BE FOUNDED.

BY GEORGE H. F. NUTTALL, F.R.S.,

*Quick Professor of Biology, Director of the Institute.*

(With Plates IV—VI and 6 Text-figures.)

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## INTRODUCTION.

THE foundation of an Institute for Research in Parasitology in Cambridge is an achievement worthy of being recorded in some detail since it affords a recognition of the value of a branch of biological science that cannot but

gratify all who have gained an insight into the deep significance of the many problems which parasitology presents when viewed from the standpoint of pure science.

We should, moreover, signalize the generosity of the benefactors who have rendered possible the establishment of such an Institute, for the help they have given deserves the gratitude of all who are concerned directly or indirectly in securing the welfare of man, animal or plant by combating the parasites which are the cause of so much waste and death throughout the living world.

## I. EVENTS ANTECEDENT TO THE FOUNDATION OF THE INSTITUTE.

Since the writer's tenure of the Quick Professorship of Biology has had an important bearing upon the developments which led to the foundation of the Institute, it seems appropriate, in the first instance, to dwell upon the history of the Professorship and the conditions that apply to its tenure. Moreover, the work done in the Quick Laboratory during the years 1907–19 led by a process of natural growth to the inevitable necessity for the more favourable accommodation that has since been found in the Molteno Institute.

The will of Frederick James Quick[1] bequeathed to the University of Cambridge a fund called the *Frederick James Quick Fund*[2], the income thereof to be devoted to the promotion of "study and research in the sciences of vegetable and animal biology." The administration of this fund was entrusted by the testator's trustees to a Board of Managers consisting of the Vice-Chancellor and six Members of the Senate of the University appointed by Grace. The income of the fund was to serve (*a*) mainly for the stipend of a Chair (£1000) to be called the *Quick Professorship of Biology*, and (*b*) for the expenses of research carried on in the Professor's laboratory. The Quick Professorship is tenable for three years from the date of election, the latter taking place triennially and being open to all who may apply. The writer has been elected to five successive triennial periods of tenure. At the end of the first and second triennial periods an interval of six weeks occurred during which the chair was vacant and the stipend ceased, but the regulations governing the chair were modified in 1918[3] by advancing the date of re-election so that there should be no break in the tenure of the Professorship.

The original regulations governing the Quick Professorship[4] provided *inter alia* "that it shall be the duty of the Professor to devote himself to the study of the Protozoa, especially such as cause disease, and generally to promote that branch of science by research and by the superintendence of a laboratory or otherwise." The regulations provided, moreover, that the chair might "at

[1] For biographical note relating to Mr Quick, see p. 100.

[2] See *Cambridge University Reporter*, 3, II. 1903; 33, III. 1906, pp. 577–581; 1, v. 1906, pp. 778–781.

[3] *Ibid.* 23, IV. 1918, p. 619.

[4] *Cambridge University Reporter*, 13, III. 1906, p. 579.

any time after twelve years from the election of the first Quick Professor be subject to alteration by Grace of the Senate on the recommendation of the Board of Managers."

It may be mentioned here that the regulations were modified in 1920[1] on the recommendation of the Managers of the Quick Fund whereby the regulation cited in the previous paragraph was altered, the words "it shall be the duty of the Professor to devote himself to the study of the Protozoa, especially such as cause disease," being changed so as to read "it shall be the duty of the Professor to devote himself to the study of Parasitology." The Managers recommended that the field of study and research should be *Parasitology* for the following reasons:

> Parasitology includes, of course, the study of Protozoa causing diseases as a special section. As a pure science it is closely linked up with vegetable and animal biology generally, while as an applied science it appeals equally to the medical man, the veterinarian and the agriculturalist.
>
> Professor Nuttall has now been elected Quick Professor for periods of three years, five times in succession, and the work continuously carried out by him, and under his direction, has insensibly drifted into the wider field of Parasitology.
>
> Hitherto there has been no suitable laboratory available for the Quick Professor of Biology. The authorities of the Medical School placed the unfinished part of their Museum at his disposal, temporarily, but even then the Professor and his staff have been crowded into what is practically one room. It is a happy solution of this difficulty that a new Institute has been given to the University, planned expressly for the continuation and expansion of the work of the Quick Professor.
>
> As Professor Nuttall has been so closely associated with the gift to the University of the Molteno Institute for Research in Parasitology it seems to the Managers of the Quick Fund desirable to extend the field of activity set down for the Quick Professor so that it may coincide with that for which the Research Institute is destined.
>
> Regulation 11 for the administration of the Quick Fund provides for alteration of the other regulations except nos. 1, 2, 7, 10 and 11 at any time twelve years after the date of the first election (16th October, 1906), "provided that in all cases the main object of the Fund, namely, the promotion of study and research in the sciences of vegetable and animal biology shall be adhered to." The alteration of regulation 8 (1), now proposed, is entirely in keeping with the main object of the Fund.

*The Quick Endowment for Research.* As previously mentioned (see p. 98), the Quick Fund, which provides the stipend of the Professor, also makes a certain provision for the expenses of research carried on in his laboratory. This fund, during the years 1906–18, yielded an average annual income of about £200 which has since increased to £300. Until the foundation of the Molteno Institute this represented the sole permanent source of income available for the purposes of research and the maintenance of a laboratory.

[1] *Cambridge University Reporter*, Date of Report 2, XII. 1920.

## FREDERICK JAMES QUICK (1836–1902).

### A Biographical Note.

(With portrait, Plate IV.)

Mr Quick was born in London on 22nd October, 1836, as the second son of James Carthew Quick, a wholesale coffee dealer of that city. He was educated at Harrow (1851–55) and Trinity Hall, Cambridge, where he came into residence in October, 1855, and took the degree of B.A. on 29th January, 1859. He studied for the Bar, but never practised. He learned farming at St Andrews, his father buying Woodmancole at Elmsworth, Sussex, for him. For a short time he became partner in a wholesale tea business, and in 1869 he entered (again as a partner) the firm of Quick, Reed and Smith, which his father had founded. He remained the head of this firm until his death on 21st December, 1902. Shortly before his death, having a horror of being buried alive, he requested one of the trustees of his will[1], Mr Williams, to see that "a surgeon probed his heart to see that death had taken place," asking, moreover, that his body might be cremated. His wishes were duly carried out, and his ashes were buried at Broadwood Cemetery. Mr Quick never married.

In business Mr Quick was a shrewd, far-seeing, and capable manager. His associates were greatly impressed with the accuracy of his judgment in affairs and in the estimation of the character of those with whom he came in contact.

He was much interested in botany and biology, and to this the founding of the Quick Professorship is mainly to be ascribed. Mr Williams has informed the writer that Mr Quick was very anxious that the Chair should be always abreast of the times, this accounting for pertinent provisions in the bequest. The full benefit of the latter will not be realized until the expiration of certain life-interests.

The writer is greatly indebted to Mr J. W. Williams for providing most of the information on which this note is based; Dr Henry Bond, Master of Trinity Hall, kindly supplied the little that is recorded in the College books.

## THE QUICK LABORATORY.

After being elected to the Quick Professorship, the writer found "temporary accommodation" in the unfinished portion of the Medical School Museum, establishing the "Quick Laboratory" therein. The temporary quarters, however, became quasi-permanent for they were occupied during the years 1907–21. The laboratory consisted of one large room (Fig. 1) which was divided into cubicles by means of matchboard partitions and suitably placed cupboards or screens, the accommodation being the best that was available. A wooden floor was erected over that of the museum so as to bring the work benches near to window-level, the result being that the floor was very resonant, apart from its being creaky owing to its light sub-structure. The room grew inadequate at an early date for the increasing number of workers, collections, books and apparatus. The number of persons working in the room rendered

[1] Mr Quick's second Trustee is Mr John Eagleton of London.

FREDERICK JAMES QUICK

1836—1902

Founder of the Quick Professorship of Biology, Cambridge

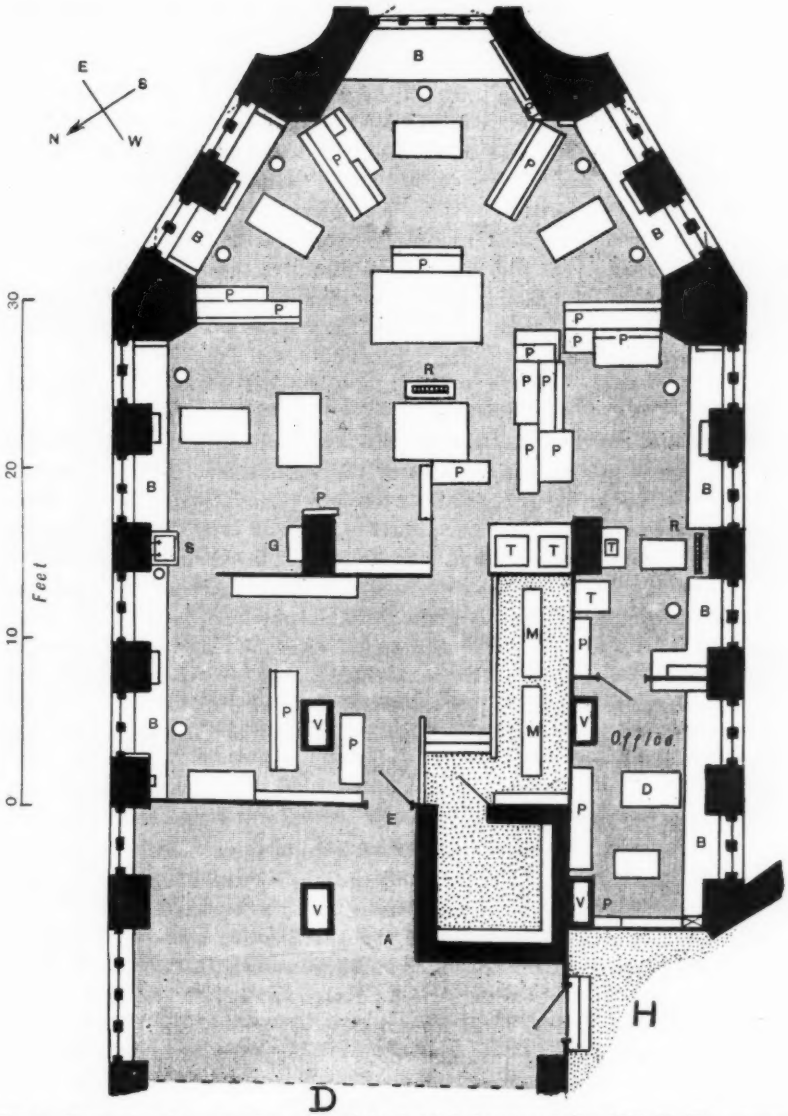



Fig. 1. Illustrating the cramped quarters of the Quick Laboratory during 1907–21. The entrance to the Laboratory (E) is reached by passing through the Hall (H) and small Demonstration Room (D) of the Medical School. The lettering indicates the internal arrangements: Alcohol specimen room (A), Benches (B), Desk (D), Glass blower (G), Microphotographic apparatus (M), Presses, Cupboards, Book-cases and Cabinets (P), Radiator (R), Sink (S), Thermostats (T), Ventilating shafts (V), Tables and shelves are left blank and 9 work-places are indicated by circles opposite benches.

it a very noisy place where through the shifting about and conversations going on it was difficult to collect one's thoughts and to carry on experimental work without constant interruptions, privacy being precluded. There was but one sink in the room for all the workers, there was danger of fire because of the amount of woodwork and alcohol-preserved material, and finally, especially during the war, the lack of heating and ventilation became insupportable. It was then that the writer resolved to issue an appeal for help and proceeded to write out a statement showing what a need there was in Cambridge of a suitably equipped Institute for Parasitological Research, the Quick Laboratory, in addition to all its other failings, being a place totally unfit for the prosecution of researches on organisms of an infective nature. The Quick Laboratory, as such, has ceased to exist since it is now incorporated in the Molteno Institute.

*Scientific Staff of the Quick Laboratory.*

With the aid of the grants and benefactions to be mentioned (p. 104) the following scientific staff was established, the various posts being created by Grace of the Senate: In June, 1907, a *Research Studentship in Medical Entomology* was established with an annual stipend of £100 derived from the Tropical Diseases Research Fund[1]. In December, 1908, an *Assistantship in Protozoology to the Quick Professor* was established with an annual stipend of £100 paid during three years by the writer and subsequently by grants which have since been augmented[2]. A second *Assistantship* was subsequently established but has lapsed. In November, 1911, a *Demonstratorship in Medical Entomology* with a stipend of £50 was established[3] and in 1913–14 the post of *Helminthologist* was created with a stipend of £100, derived during the first year from laboratory funds[4].

*A List of those who worked in the Quick Laboratory* 1907–21.

Since it may be of interest in the future, a list of those who were engaged in research in the Quick Laboratory is herewith appended, the names of those who have published papers being marked with an asterisk:

*Professor:* *G. H. F. Nuttall, F.R.S., 1906–21; *Demonstrator:* *C. Warburton, M.A., F.Z.S., joined in 1908, appointed 1911; *Assistant:* *H. B. Fantham, Sc.D. (London), 1908–10; *C. Strickland, M.A., B.C., 1910–12; *K. R. Lewin, B.A., 1912–13; *E. Hindle, M.A., Ph.D., joined 1910, appointed 1913–17; *D. Keilin, Sc.D. (Paris), joined 1915, appointed 1917; *Helminthologist:* *Miss Annie Porter, Sc.D. (London), joined 1908, appointed 1913; T. Storrar Cave, B.A., 1914; *Research Student in Medical Entomology:* A. H. Lees, B.A., 1907;

[1] *Cambridge University Reporter*, 11, VI. 1907.

[2] *Ibid.* 1, XII. 1908, p. 263; 24, XII following (Grace). Stipend now paid from the Tropical Diseases Research Fund, Medical Grant Committee and Medical Research Council.

[3] *Ibid.* 10 and 24, X., 14 and 21, XI. 1911. Stipend paid by the Tropical Diseases Research Fund.

[4] Stipend paid in 1914 by the Tropical Diseases Research Fund. Owing to the war, the post has since been in abeyance.

*F. P. Jepson, B.A., 1908–9; *G. Merriman, 1909–12; *N. Cunliffe, B.A., 1913–14; M. E. MacGregor, B.A., 1914–15; *D. Keilin, Sc.D. (Paris), 1915–17, when he became Assistant and the Studentship was merged with the Assistantship he now holds.

Other workers in the Laboratory were: G. Beatty, M.D., Medical Officer, South Nigeria, 1911; Dr de Blieck, Director Veterinary Department, Java, 1915; Y. Bogaerts, medical student from Louvain, 1915; Major J. E. M. Boyd, M.C., R.A.M.C., sent by the War Office, 1919–20; *P. A. Buxton, M.A., now of the Health Department, Jerusalem, 1920; *Mr G. W. Bullamore, Director of the Institute for Bee-keeping, 1920–21; Major S. R. Christophers, I.M.S., Superintendent, King Institute of Preventive Medicine, Madras, 1912; *Major J. W. Cornwall, M.D., I.M.S., Pasteur Institute, Coonoor, South India, 1912; Captain J. D. Coutts, M.R.C.V.S., D.V.S.M., South Rhodesia, 1921; *Dr Lajos Gózony, Assistant, Bacteriological Institute, University of Budapest, 1914; Dr Graham, Medical Officer, Gold Coast, 1907; *Dr S. Hadwen, Pathologist, Biological Station, Ottawa, Canada, 1908–9, 1913; *L. Harrison, B.Sc., University of Sydney, Australia, 1914–16; Dr A. D. Hodges, Principal Medical Officer, Uganda, 1910; *F. M. Howlett, B.A., Assistant Imperial Entomologist, India, 1910; *Dr J. C. Johnson, Professor of Biology, New Zealand, 1913; Dr F. I. M. Jupe, Medical Officer, Gold Coast, 1910; R. C. Lewis, M.A., Cape Colony, 1911–12; Miss Jordan Lloyd, Newnham College, Cambridge, 1911; F. J. McCall, M.R.C.V.S., Veterinary Officer, British East Africa, 1914; N. MacDonald, Veterinary Service, Australia, 1909; *Miss D. Mackinnon, B.Sc., Carnegie Scholar, Aberdeen, 1908; J. E. M. Mellor, B.A., 1915, 1919; Dr C. de Meza, Veterinary Officer, Nyasaland, British East Africa, 1916; A. R. Momber, 1910–11; J. O. Muñoz, medical student from Liège, native of Mexico, 1914; *Captain J. W. Munro, B.Sc., R.A.M.C. (temp.), sent by War Office, 1917–19; *Dr Lucius Nicholls, Pathologist, Victoria Hospital, St Lucia, W. Indies, 1912–13; Dr Erik Nordenskiöld, Lecturer in Zoology, University of Helsingfors, 1910; *Captain W. S. Patton, M.B., I.M.S., 1908–9; I. M. Puri, M.Sc., Punjab, India, research student, 1921; L. P. W. Renouf, B.A., Trinity College, Cambridge, 1914; *L. E. Robinson, A.R.C.S. (London), research student, 1919–21; *Dr P. H. Ross, Government Bacteriologist, Nairobi, British East Africa, 1914; L. G. Saunders, M.Sc., McGill University, Montreal, research student, 1921; L. D. Sayers, B.A., Downing College, Cambridge, 1914; Dr J. O. Shircore, Medical Officer of Health, Nyasaland, 1914; *Dr G. S. Graham-Smith, Cambridge, 1908; *Dr G. U. Smith, Egypt, 1908; *Major F. H. Stewart, M.D., Sc.D., I.M.S. (retired), 1920–21; *Dr N. H. Swellengrebel, Assistant in Protozoology, Hygenic Institute, Amsterdam, 1910; J. F. Valladares, Senior Lecturer, Government Veterinary College, Bombay, 1910; Miss W. M. Vincent, Newnham College, research student, 1921; Major C. E. Williams, M.D., I.M.S., Rangoon, 1911; K. P. Williamson, M.A., Indian Education Service, 1911; Dr J. Y. Wood, Medical Officer, Kaballa, Sierra Leone, 1914; *Dr Wu Lien-Teh, Army Medical College, Tientsin, China, 1912;

Dr T. Yamanouchi, Tokio, Japan, 1910; Dr S. Yoshida, Department of Pathology, Osaka University, 1920.

*Work carried out in the Quick Laboratory.*

During the years 1906–21 the publications that emanated from the laboratory numbered 216, a large proportion appearing in this Journal. Some of the research work was done for Governments, notably that on piroplasmosis and East Coast Fever for the Governments of Cape Colony and Transvaal; that on the bionomics of houseflies, on fleas in connection with rat-plague, and on lice (in the first instance) for the Local Government Board; that on bee disease for the Board of Agriculture; that on lice and scabies for the War Office, the latter having been aided in drawing up Army Council Instructions dealing with lousiness and itch among troops and the methods of combating these widespread evils. "Combating Lousiness among Soldiers and Civilians" to the number of 250 copies (reprinted from *Parasitology*, x. No. 4, May 1918, pp. 411–586, 4 pls., 26 text-figs.) and issued in a special cover were presented by the writer to the British and Allied Army Medical Corps during the war.

Apart from the foregoing may be mentioned researches on bugs in relation to relapsing fever, on fleas and lice as carriers of rat trypanosomes, on the bionomics and structure of anopheline mosquitoes and their relation to malaria in England, on heartwater in sheep and goats, on piroplasmosis in the dog and horse, on the discovery of a remedy (trypanblue) for piroplasmosis and scientific observations on the effects of the drug, on the monographic treatment of the subject of ticks and of the louse, without mentioning other parasitological papers dealing with pathogenic protozoa, etc.

The activities of the Quick Laboratory were not confined to researches, for the writer, as its representative, served on various advisory bodies, notably as (*a*) Member of the Advisory Committee for Plague Investigations in India appointed by the Secretary of State for India, the Royal Society and Lister Institute; (*b*) Member of the Epizootic Abortion Committee of the Department of Agriculture and Fisheries; (*c*) Member of the Honorary Committee of Management of the Imperial Bureau of Entomology, Colonial Office; (*d*) Member of the Government Grant Committee for Scientific Investigations, Royal Society; (*e*) Member of the Fish Preservation Committee of the Department of Scientific and Industrial Research; (*f*) Member of the Army Pathology Advisory Committee, War Office. As usual, these various services have been rendered gratuitously.

## REGARDING VARIOUS GRANTS AND BENEFACTIONS IN AID OF RESEARCH.

The income of the Quick Fund proving insufficient, the writer found it necessary to obtain financial assistance from outside sources, no funds being available from the University. For several years he defrayed the extra cost including the payment of the University Assistant to the chair and a Secretary.

Since 1909, annual *Grants* have been derived continuously from the Tropical Diseases Research Fund (Colonial Office), three grants were obtained from the Local Government Board (1913–16), three from the Board of Agriculture (1915–17) and one from the Rockefeller Institute, New York (1913–14), whilst, since, 1917, grants have been received from the War Office (once), and (repeatedly) from the Medical Research Council and Medical Grant Committee (Ministry of Education).

In addition to the foregoing, various *Benefactions* were received from private and other sources as follows: In 1909–10, from The Transvaal Government, £500; The Government of Cape Colony, £500; The Duke of Bedford, £100; Lord Rothschild, £100; Sir Richard Cooper, Bart., £100; Mr and Mrs P. A. Molteno, £100; Harry Mosenthal, Esq., £26. 5*s*.; J. Buchanan, Esq., £25; The Tropical Diseases Research Fund, £25; E. Darwin, Sc.D., F.R.S., £5. 5*s*.; Julius Auerbach, Esq., £5. 5*s*.; Fred C. Norton, Esq., £2. 2*s*.; making a total of £1489[1]. In 1914, from Mr and Mrs P. A. Molteno, £400 (£100 thereof toward expenses of publication); Sir Dorabji J. Tata, £250; Mr and Mrs Henry Bubb, £25; making a total of £675[1].

### THE FIELD LABORATORY.

In 1909–10, largely through the above-mentioned benefactions, a field laboratory was erected by the writer upon the Milton Road at a distance of two miles from the Medical School and present site of the Molteno Institute, the laboratory serving for experimental researches that cannot be carried out in the town. The buildings are of a temporary character but ample to meet the needs of the Institute in the future; they form an essential annex to the Institute. Our laboratory can accommodate two to four research workers, being adequately and economically heated by hot water radiator pipes and a coke furnace, water and gas being laid on but not electricity. The site of our laboratory forms a part (about 5 acres) of the University Field Laboratories comprising 27 acres of land. (See Fig. 2, showing the general distribution of the buildings.)

## II. THE FOUNDATION OF THE MOLTENO INSTITUTE.

The highly unsatisfactory conditions prevailing in the Quick Laboratory led the writer to issue an appeal for funds with which to erect an Institute for Parasitological Research in Cambridge. The appeal was issued in printed form in May 1919 for private circulation[2]. From Mr and Mrs P. A. Molteno it evoked the following generous response which was subsequently published in the *Cambridge University Reporter* by the Vice-Chancellor:

[1] See *Cambridge University Reporter*, 22, II. 1910 and 9, VI. 1914.

[2] Nuttall, G. H. F. (1919), *The Need of an Institute for Parasitological Research in Cambridge*, 19 pp. 28 × 22 cm. (Illustrated with a general view and plans of the proposed Institute, Quick Laboratory and Field Laboratory. Privately printed at the University Press, Cambridge.)

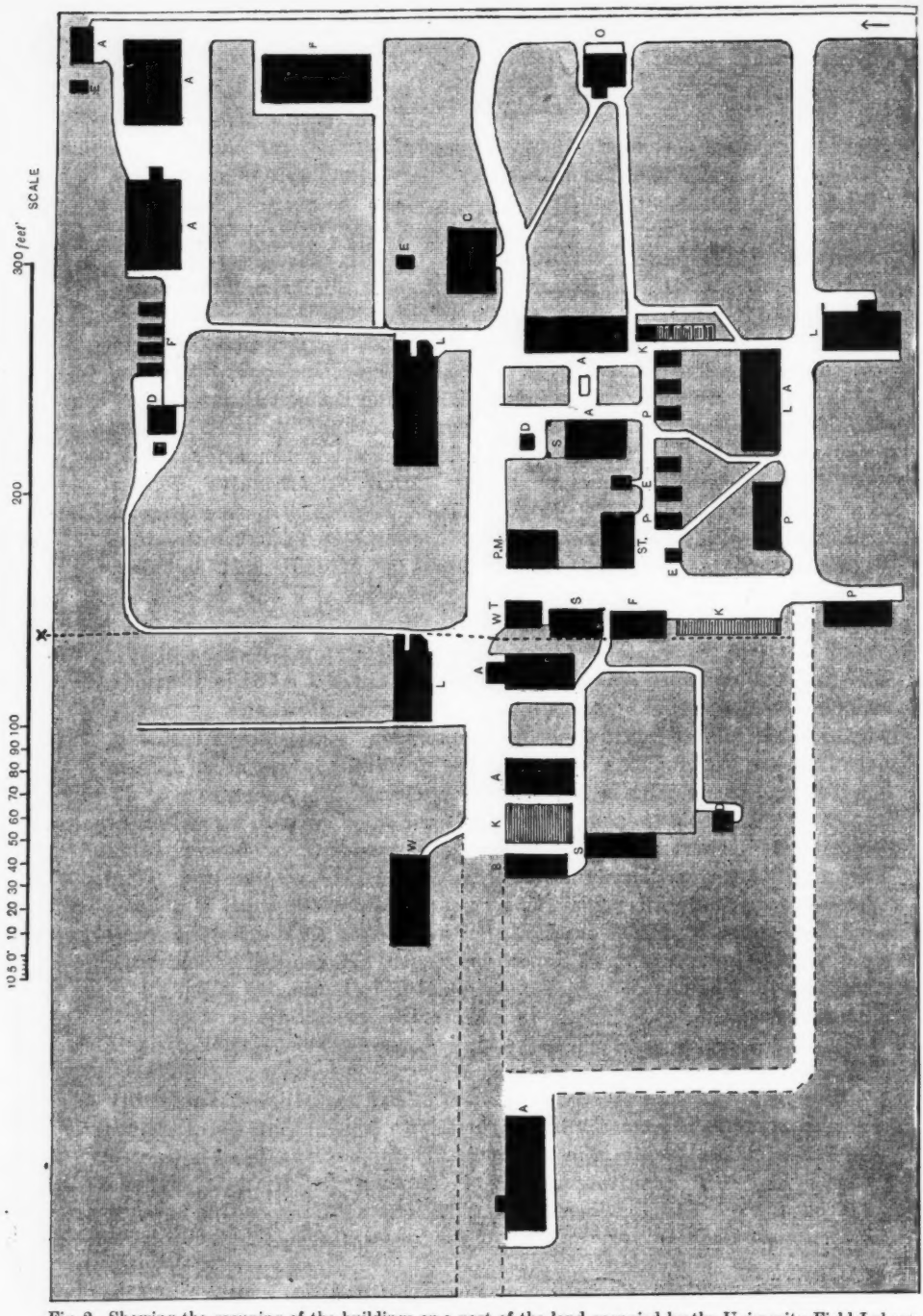
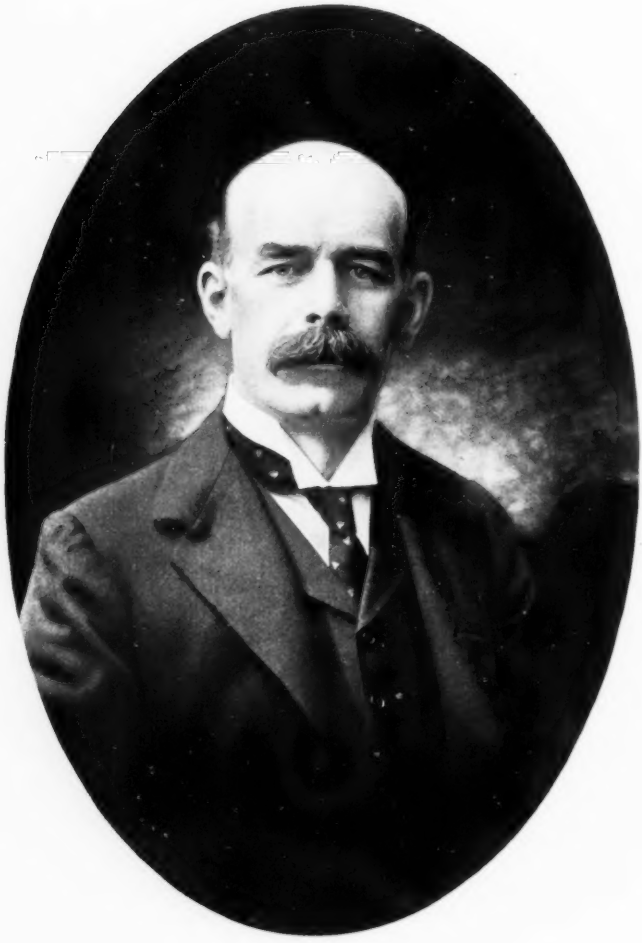



Fig. 2. Showing the grouping of the buildings on a part of the land occupied by the University Field Laboratories, Milton Road, Cambridge. The dotted line (X) indicates the eastern boundary of the land belonging to our Laboratory as distinguished from that of the Agricultural and Pathological Departments; some of the buildings being held in common. Except for one building (below, on figure) to the extreme west, belonging to the Pathological Department, all buildings to the west of the dotted line belong to our Laboratory. The different structures are indicated by letters: (A) cattle sheds and stables, (C) caretaker's cottage, (D) destructor, (E) earth closet, (F) fodder store, (K) concrete platform, (L) laboratory, (O) office, (P) piggeries, (P.M.) autopsy house, (S) shed, (ST.) stable, (WT.) weighing-house.



PERCY ALPORT MOLTENO

1922

## MR AND MRS P. A. MOLTENO'S BENEFACTION.

EMMANUEL COLLEGE LODGE. 1 *November*, 1919.

The Vice-Chancellor has pleasure in publishing to the Senate the following letter which has been received by Professor Nuttall:

10, Palace Court,
London, W. 2.
*October 23rd*, 1919.

*Professor George H. F. Nuttall, F.R.S.,*
*Longfield,*
*Madingley Road,*
*Cambridge.*

Dear Professor Nuttall,

I have for long been interested in your work on parasitology. I regard this work as of the very greatest value to the Empire and particularly to Africa, the home of so many diseases transmitted by and through parasites.

Your researches have already produced results which are of immense benefit in the control and prevention of diseases both of men and of animals. Indeed research of this nature is indispensable if Africa is to be made habitable for white men and for animals of European stock.

Your researches are however not bounded by the African field, vast as it is, but will apply all the world over in alleviating human suffering and protecting human and animal life from disease.

I am well aware how utterly unprovided you are with the necessary accommodation to carry on research work. It is really a scandal that this should have been allowed to continue for so long, and the difficulty grows continuously with the increase in the number of your specimens and the extension of your work.

Mrs Molteno has also been greatly interested in your work and desires to join me in providing funds for the erection and maintenance of a suitable building to be used in the future as an Institute for parasitological research in the University of Cambridge.

We understand from you that you consider a sum of £20,000 would provide a suitable building with its fittings for this work, and that a further sum of £10,000 would be necessary as a fund to provide an income for the upkeep and maintenance of the Institute, and that any surplus from this income could be used with the greatest advantage in furthering the purposes of research to be carried on in the Institute.

Mrs Molteno and I will be glad to present to the University these sums of £20,000 and £10,000 making £30,000 in all for these purposes, on the understanding that the University is prepared to provide a suitable site. We desire that this sum should be a benefaction to the University for the purposes outlined above.

After provision for the upkeep of the fabric, the balance of the income available from the maintenance fund should be placed at the disposal of the Director of the Institute (in the first place yourself) to be used at his discretion in furthering the work of research.

We desire further to say that we have examined the plans drawn up by Mr Harry Redfern, F.R.I.B.A.—with the general view of the proposed Institute as it would appear on the Downing site at Cambridge. These plans appear to us to afford a suitable building, with the various halls for Library, Museum, etc. and rooms for Professor and students carrying on research work.

Accommodation appears to be provided without any unnecessary superfluities in bricks and mortar, and yet to be simple and dignified, and we hope it will be found possible for this plan to be carried out.

I will be obliged to you if you will convey the contents of this letter to the Vice-Chancellor for communication to the Senate, and to the Cambridge University Association.

I may conclude by saying that I am a member of Trinity College, Cambridge, and an M.A. and LL.M. of the University, and that I have always had the highest regard for the University, and for the great work which it has done and is carrying on, and I am very glad to have the opportunity, in some small way, to assist in extending that work.

Believe me,
Yours faithfully,
P. A. Molteno.

This great benefaction was followed by a second of £6000, likewise from Mr and Mrs Molteno, to meet the greatly increased cost of building that became apparent as soon as the estimates were worked out[1].

It may be noted here that Mr and Mrs Molteno had already helped on the work of the Quick Laboratory financially in 1909 and 1914 (see p. 105) and that throughout the intervening years they had evinced much sympathy and interest in the researches carried out in our laboratory.

The foregoing benefaction led to another which otherwise would not have been received. It was announced in the *Cambridge University Reporter* as follows:

BENEFACTION FROM THE LATE LORD STRATHCONA AND MOUNT ROYAL.

EMMANUEL COLLEGE LODGE. 20 *November*, 1919.

The Vice-Chancellor has pleasure in informing Members of the Senate of a further benefaction received, on November 18, by Professor Nuttall:

In the *Cambridge University Reporter* of 22 February, 1910, under the heading "Benefactions for Research Work in Parasitology," the Vice-Chancellor informed Members of the Senate that various donations had been received by Professor Nuttall for the purposes of a field laboratory on the outskirts of Cambridge, adding that "£1000 has been promised, anonymously, when the fund has reached £6000."

This promise emanated from the late Lord Strathcona and Mount Royal, who visited Cambridge in July, 1909, and evinced much interest in the parasitological work that was being carried on in the University.

When Mr and Mrs P. A. Molteno generously offered the sum of £30,000 for the purpose of building and maintaining an Institute for Parasitological Research in Cambridge (*Reporter*, 4 November, 1919, page 206), an offer since accepted by Grace of the Senate, Professor Nuttall communicated with the late Lord Strathcona's representatives, with the result that Lady Strathcona asked the Executors to pay Professor Nuttall the sum of £1000 "conditionally promised as a contribution to the Biological Research Laboratory (now the Institute for Parasitological Research) in connexion with Cambridge University."

## THE INAUGURATION CEREMONY.

Before describing the new Institute in detail an account may be given of the ceremony of its inauguration.

The Institute was opened on the afternoon of 28th November, 1921[2], by Earl Buxton of Newtimber, G.C.M.G., late Governor-General of South

[1] See *Cambridge University Reporter*, 20, XII. 1920, p. 130.

[2] Before the opening ceremony, visitors from the outside were entertained at lunch parties given respectively by the Vice-Chancellor and Mrs Pearce at Corpus Christi College, Sir Arthur Shipley and the writer at Christ's College, Dr and Mrs H. K. Anderson at the Lodge of Caius College and by Mr and Mrs P. A. Molteno at the University Arms Hotel.

ELIZABETH MARTIN MOLTENO *née* CURRIE

1921

Africa, under the Chairmanship of the Vice-Chancellor of the University of Cambridge, Rev. E. C. Pearce, D.D., Master of Corpus Christi College. Academic dress and decorations were worn, Doctors appearing in scarlet robes in recognition of the importance of the occasion, a large and distinguished audience being present.

The Molteno family were represented by Mr and Mrs Percy A. Molteno (the founders), Sir James Molteno, K.C., Admiral Molteno, C.B. and Mrs Molteno, Mr and Mrs D. J. Molteno, Captain and Mrs Lenox Murray (née Molteno), Miss Audrey Molteno, Miss E. M. Molteno, Mr H. V. Molteno, accompanied by Mrs F. C. Selous, M. Emile Coué of Nancy, Miss E. Cowan and Mr H. B. Johnson.

Foreign institutions were represented by Professor M. Caullery of the Faculté des Sciences, la Sorbonne, Paris, and Dr M. Langeron of the Laboratoire de Parasitologie, École de Médecine, Paris, both of whom came to Cambridge to attend the ceremony; and Johan Hjort, Sc.D., Professor of Marine Biology in the University of Christiania.

Among the distinguished British visitors were Lord Pentland of Lyth, G.C.S.I., G.C.I.E., formerly Governor of Madras; Sir Richard Cooper, Bart., M.P.; Sir Herbert Read, K.C.M.G. (Colonial Office); Dr S. Monckton Copeman, F.R.S. (representing the Ministry of Health); Dr Andrew Balfour, C.B., C.M.G., and Dr C. M. Wenyon, C.M.G., both of the Wellcome Bureau of Scientific Research, London; Dr S. A. Neave of the Imperial Bureau of Entomology; Dr C. L. Boulenger and Dr F. J. Meggitt of the University of Birmingham; Lieut.-Colonel S. P. James, I.M.S. (retired) of the Ministry of Health; Dr G. A. Baylis and Rev. James Waterston of the British Museum (Natural History Department); D. Ward Cutler, M.A. of the Rothamsted Agricultural Station; Dr G. H. Macalister, Principal of Singapore Medical College; Dr P. Manson-Bahr, D.S.O., of the London School of Tropical Medicine and Mrs Manson-Bahr.

Cambridge was represented by the Mayor and Mayoress and numerous members of the University including Heads of Colleges, Professors, and others with their ladies. The total number of guests being about two hundred and fifty.

The writer was unfortunately unable to attend the opening ceremony through illness, having had five days previously a severe haemorrhage from a duodenal ulcer. His absence was especially regrettable because it prevented him from expressing publicly his gratitude to the founders of the Institute, welcoming the visitors, and participating in a ceremony that represented for him the consummation toward which he had striven for many years. His disappointment was, however, greatly mitigated by the kind expressions of sympathy received from those who attended the meeting and which emanated from all the speakers on that occasion.

The opening ceremony lasted one hour and it took place in the Research Museum of the Institute, the small platform being occupied by the Vice-

Chancellor, Mr and Mrs P. A. Molteno, Earl Buxton, Lord Pentland, Sir Arthur Shipley, Professor Caullery and the Mayor of Cambridge. The speeches were brief and may be summarized as follows:

The Vice-Chancellor[1] welcomed the founders to the Institute they had brought into being and thanked them warmly on behalf of the University for their noble benefaction, stating that he "could conceive of no more worthy object for generous-minded men to spend their money on than an Institute for Research of that kind, which necessarily must in some sense ameliorate the lot of mankind." He read a telegram from General Smuts which Mr Molteno had received through the High Commissioner of South Africa; it ran:

> The Union of South Africa welcomes the opening of the Molteno Institute, which Institute is made possible by the generosity of the Molteno family. The progress of the Institute will be sympathetically watched by South African scientists.

The Vice-Chancellor had that morning received a letter of congratulation and good wishes from Dr Edmond Sergent, Director of the Institut Pasteur of Algiers, whilst Professor Nuttall had been the recipient of a telegram which ran:

> Institut Pasteur et Société Pathologie Exotique Paris adressent à Institut Molteno et à son éminent Directeur cordiales félicitations et vœux de prospérité (signed) Roux, Calmette, Mesnil.

Mr Cecil Warburton, who spoke on behalf of the writer, welcomed the representatives of the Colonial Office, Ministry of Health, and War Office, and those who had come from various universities and scientific institutions. He dwelt briefly on the main features of the new Institute and the plans that were being matured for its future development as a centre for research and advanced instruction in the whole domain of parasitology.

Mr P. A. Molteno, whose rising to speak was welcomed by loud applause, after referring in the friendliest manner to the writer, expressed his and Mrs Molteno's cordial approval of the way in which their benefaction had been applied in the construction and arrangement of the building. He referred to the very inadequate facilities which had hitherto existed for parasitological research in Cambridge and to the importance of such work for the Empire, judging by his own experiences in Africa. His eloquence, that of the practised speaker, greatly appealed to the audience.

Earl Buxton spoke as an old friend of the founders who by birth were connected with South Africa, the name of Molteno having for long been well known and respected there, "especially since the time of the first Prime Minister of Cape Province, Sir John Molteno," moreover, Mrs Molteno's father, Sir Donald Currie, had done much to assist in the development of the country. His Lordship referred to the generosity of the benefaction conferred on the

[1] The following abstracts of the speeches delivered on the occasion are made from a shorthand report.

University and to his own experience of the ravages of disease in Africa, of its certainly having been high time that such an Institute, "worthy of Cambridge," should be erected and given a local habitation and a name. "Cambridge afforded ideal conditions for the establishment of a research institute of that description, because of its many-sided scientific activities and its constant stream of young and talented men who passed through the University." He emphasized the value of parasitological research and of such an institute for the Empire: "What is very greatly required is a centre where men can be trained in the scientific methods of research which bear so greatly on the health of men, animals and plants, by receiving a broad, thorough training, for at present there is very little opportunity, except for a very few men, of obtaining such training. The training is often too slight and too diffuse, the student picking up scraps here and there in professional schools, whether medical, veterinary or agricultural. The student therefore acquires no real foundation upon which to base his future research work."

"Unfortunately, in consequence of lack of training in these respects, unripe and poorly trained men went into practice who were not really fit to investigate a scientific problem. As Professor Nuttall had said: 'They travel with blinkers on their eyes along the old well-worn professional road and too often never leave it.' Thus it may come about that insufficiently trained men are frequently given posts or are sent on research expeditions, where they are expected to do scientific work, but where, not from want of zeal, but from lack of knowledge, they naturally fail.

"It would be a very great thing if the new Institute were placed in a position of being able to hold selected men to their research work until they were fit to go out as investigators and teachers. This meant, of course, considerable funds and endowments in order to keep men at work and free from financial worry for a period of years. Travelling scholarships conferred upon suitable men by their universities or Governments in different parts of the Empire would be of the utmost value to their country and mankind. If funds were available, subsidiary aid could be furnished by the Institute itself. The latter," concluded Earl Buxton, "was certain to attract men from all parts of the Empire, and scholarships or the like would be a great additional attraction. Thus a group of young and enthusiastic workers would gather round the Institute as a centre." His Lordship then declared the Institute open.

Professor Caullery, speaking in English, as the representative from France, referred to parasitology as nearly constituting a special science in the domain of biology since it bore upon an immense number of different organisms and afforded striking evidence bearing upon evolution, besides being an essential factor in the study of disease. He was glad to find one of the best of his former pupils, Dr Keilin, established at the Institute. He and his colleagues offered their congratulations and thanks to Mr and Mrs Molteno for what they had done for science and hoped that the Institute would help to bring French and British men of science into closer affiliation.

Sir Arthur Shipley, G.B.E., F.R.S., proposed a vote of thanks to those who had come from afar to help them on that memorable occasion. He wanted to add a word to what Earl Buxton had said about the necessity of further endowment. They had started a splendid building, but Cambridge had a habit of growing. The institution had grown from the Quick Laboratory to a Molteno Institute and would go on growing under the latter name. They would, and did, want further endowment. He was afraid that he was an inveterate beggar, for they had to keep the wheels going. As an American poet had said:

> I hate to be a kicker.
> I do not make for peace.
> But the wheel that does the squeaking,
> Is the wheel that gets the grease.

The assembled company then partook of tea as the guests of Professor and Mrs Nuttall and afterwards inspected the building under the guidance of members of the staff who could be readily singled out through their wearing Cambridge-blue rosettes.

## THE MOLTENO INSTITUTE FOR RESEARCH IN PARASITOLOGY.

The following account of the Institute may prove useful to others who are contemplating the establishment of similar institutions elsewhere. Since the Institute was opened, and indeed before, it has been sought by numerous visitors interested in laboratory construction and arrangements who desired information on various matters, and this account will serve to answer some of the questions that have been asked by our visitors.

### Preparations for Building the Institute.

A Syndicate was appointed on 6th December, 1919, by Grace of the Senate (*Camb. Univ. Reporter*, 9, xii. 1919, p. 355) to obtain plans and estimates for the erection of the Institute on the site assigned for the purpose (*vide infra*). This Syndicate consisted of the Vice-Chancellor (P. Giles, Litt.D., Chairman), Charles E. Grant-Ives, M.A., Rev. J. B. Lock, M.A., and G. F. C. Gordon, M.A., of the University Building Committee; G. S. Graham-Smith, M.D., F.R.S., Charles T. Heycock, M.A., F.R.S., Charles G. Lamb, M.A., and the writer (Secretary). This Syndicate held five meetings at three of which the plans were discussed with the architect, Mr Harry Redfern, F.R.I.B.A. The latter reported that the probable cost of construction, starting in March, 1920, would be £28,600 including architect's fees and disbursements, the calculations including a sum of £1500 for fittings and contingencies, the complete building (151,200 cubic feet) being reckoned to cost three shillings and seven pence per cubic foot. The Syndicate reported this to the Senate and their report was approved (*Camb. Univ. Reporter*, 3, ii. 1920, p. 582; 2, iii, 1920, p. 688; 9, iii. 1920, p. 719; 16, iii. 1920, p. 746 (Grace passed)).

Subsequently various changes in the choice of materials were made whereby the cost was reduced. Tenders for the erection of the building were received

from six contractors, that of Messrs William Saint Limited, Cambridge, being accepted (at £27,706).

## THE SITE OF THE INSTITUTE.

Building operations were begun on 10th May, 1920, upon an attractive plot of land situated on the "Downing Site," belonging to the University and so-called because it was purchased from the immediately adjoining Downing College. The south side of the building faces the grounds of the College, there being no intervening buildings, its distance from the boundary fence being 20 feet at the S.E. corner and 38 feet at the S.W. corner of the Institute, thus reserving a small strip of land to the south of the building which has in part been fenced in, and where it is hoped, with time, one or more aquarium basins, etc., may be constructed. The removal into the new Institute took place toward the end of October, 1921, whilst workmen were still engaged in parts of the building.

The Institute is very favourably situated with regard to space and remoteness from the noise, tremor and dust of street traffic. In its immediate vicinity there is being erected a Low Temperature Station, built at Government expense and intended primarily for the scientific study of refrigeration in its bearing on food preservation and allied problems. The Schools of Forestry, Agriculture, and Botany are close by, likewise the Physiological and Biochemical Laboratories, the latter being now in course of construction. Access to the Downing Site, upon which these buildings stand, is gained from Downing Street on whose opposite side lie the Medical School, Zoological and Chemical Laboratories and other University buildings which harbour the Zoological Museum, Balfour Library (Zoological) and the Library of the Cambridge Philosophical Society which the workers at the Institute frequently seek. Apart from departmental libraries in the schools and laboratories mentioned as being near at hand, the great University Library may be finally noted as being at a distance of but 10 minutes' walk from the new Institute.

## DESCRIPTION OF THE INSTITUTE.

### *The Exterior of the Building.*

The external features of the Institute have been described at my request as follows by the architect, my friend Mr Harry Redfern, F.R.I.B.A.:

"In designing the elevations of any building it is incumbent upon the architect to express, as well as he can, the use to which that building is to be put. Such limits as may be imposed upon him by the nature of the materials employed—whilst often confining his problem within some narrow limits—not infrequently exercise a restraint which is beneficial to the result.

"If the building has been planned strictly to suit its purpose, and if the elevations truly reflect the plan (as they should do) it would seem inevitable that the external appearance is predestined, and that little remains for the designer but to model the various features with care—emphasizing here,

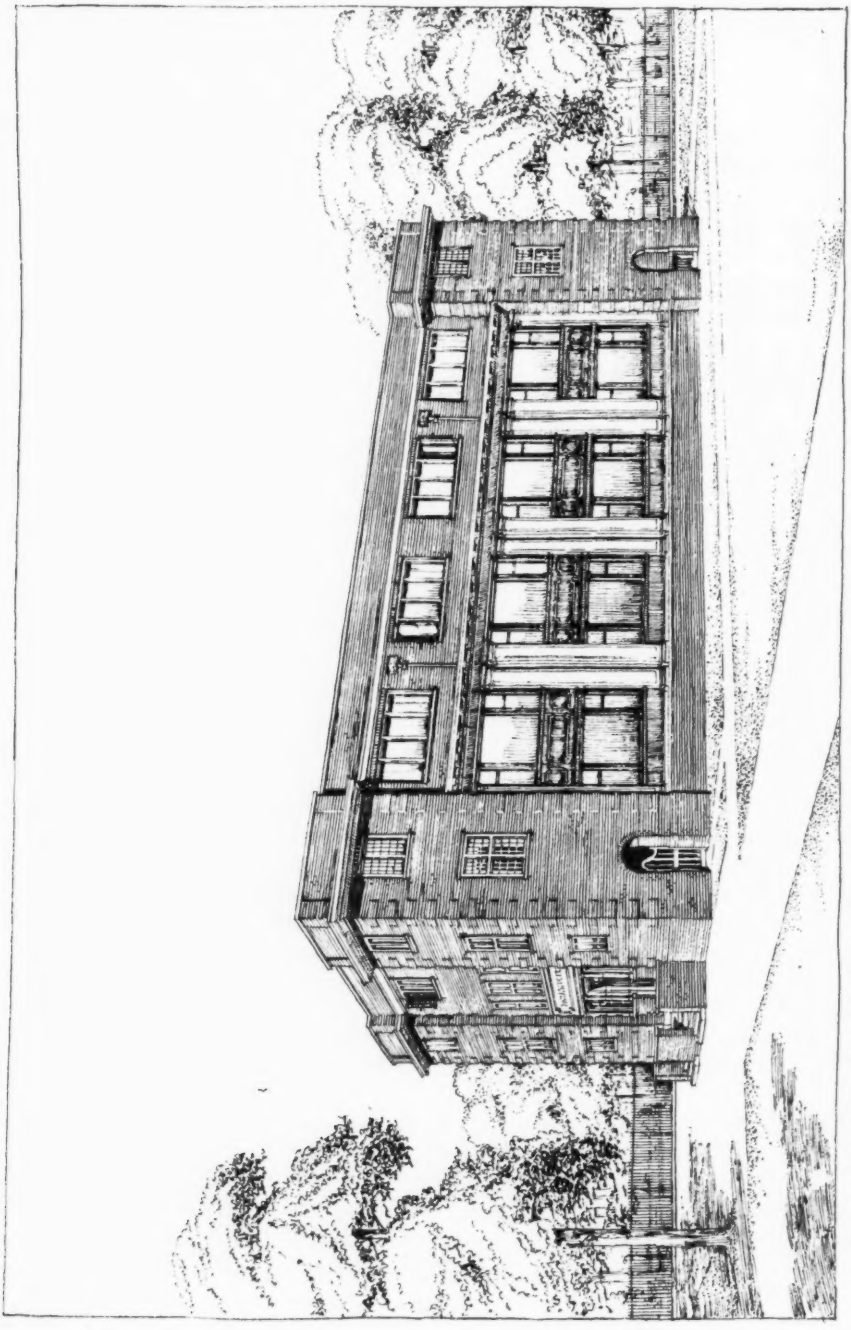


Fig. 3. General view of the Molteno Institute for Research in Parasitology, north side and east end, showing the large plate glass windows of the eight research rooms on the ground and first floors, and the four-light plate glass windows of the second floor (research museum). From a drawing executed in the architect's office since the building was erected.

toning down there—until the result satisfies his fancy. In any building the fenestration is a very powerful factor in the design.

"The buildings used by scientists for their highly technical operations present certain difficulties to their architect when designing the exterior: for example, it not infrequently happens that adjacent rooms on the same front demand entirely different conditions as to the size, number and arrangement of the windows, etc. It is such difficulties as these which make the planning of laboratories an extremely interesting problem in design. Furthermore, a building should not only be true to itself but should harmonize with its environment. It has a duty to its immediate neighbours, especially if these are buildings of a University.

"The above considerations had weight in the designing of the Molteno Institute. The architect was influenced by the expressed desire to build in brick of a certain colour and texture and to avoid the use of an undue amount of stone dressings. Moreover, the roof had to be flat, in order to admit of its being used in connection with certain work in the laboratories.

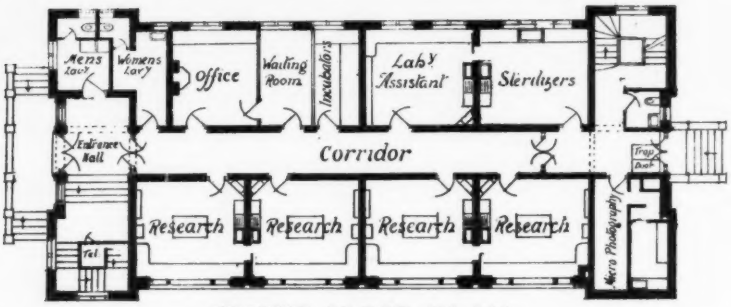
"The accompanying plans show that, broadly speaking, there are two types of room: a series of research laboratories, with one side of each consisting almost entirely of windows glazed with large sheets of plate glass; the other type a series of rooms where large windows were unnecessary and undesirable. In the midst of this series is a large library, and the top floor is, for all practical purposes, an enormous room—the Research Museum. How to combine these elements into a composition in which the large glass area of the research room windows should not throw the remainder out of scale, nor the numerous smaller windows fritter away the wall space—how they should be arranged in some rhythmical way—that was the problem of the elevations.

"It seemed best to group the research rooms together on the two floors and to combine the two storeys into one 'order' by treating the piers between the windows as pilasters, the intervening wall-surface being kept low in tone; by this means the dark masses of the large windows do not unduly assert themselves but are kept in a relatively subservient position in the strong vertical emphasis of the pilaster groups. The regular series of four-light windows on the top storey are intended to indicate the existence of one large room; whilst the treatment of the south front with its smaller windows with leaded panes and the brick piers, *quâ* pilasters, between is intended to present a kindly front to the green Court of Downing College.

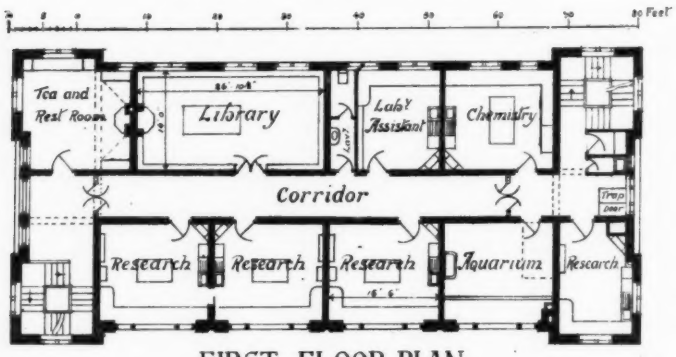
"The colour scheme of the exterior has received some consideration: it is quiet and subdued and somewhat low in tone. The brick walls are in broken tints varying from purple-brown to brownish-grey; the copings, cornices and pilasters are grey-white; the woodwork (all of teak) is fast approaching a similar tone.

"This simple building, standing four-square against a pleasant background of old trees, is an attempt to house a modern scientific department in a manner not unsuited to its needs and the 'atmosphere' of its environment."

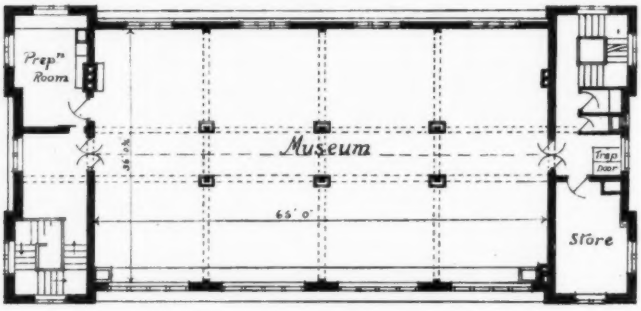
of the eight research rooms on the ground and first floors, and the four-light plate glass windows of the second floor (research museum).
From a drawing executed in the architect's office since the building was erected.



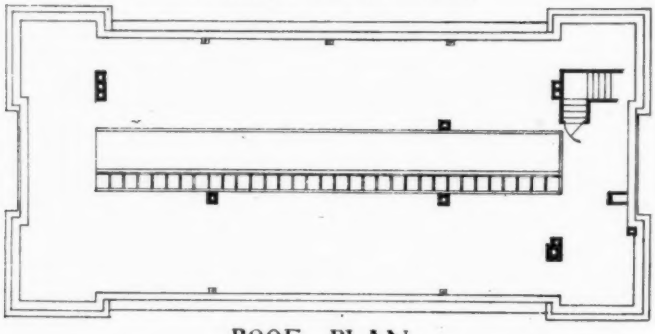

GROUND FLOOR PLAN




FIRST FLOOR PLAN




SECOND FLOOR PLAN



ROOF PLAN

Fig. 4. Plans of the Institute as completed.

*The Interior of the Building.*

The interior of the Institute was planned by Mr Redfern and the writer with a view to securing a maximum of convenience in the matter of general arrangement, light, ventilation and heating, whilst having regard to considerations of economy in view of the greatly increased cost of building operations consequent upon the great war.

*Basements.* These are restricted to both ends of the building, the basement on the east, serving for the accommodation of bicycles, being entered by a gate set in an arched doorway; this basement has a transversely ridged floor sloping downward to a level portion partly occupied by bicycle racks. The size of this basement corresponds to that of the combined area occupied by the staircase shaft, vestibule and lavatories above.

The basement to the west corresponds in size to the area covered on the ground floor by the photomicrographic room, research room, vestibule, part of the corridor, sterilizing room and staircase shaft. This basement contains the furnace and coal cellars on the north, the exit to the chute from the roof (see p. 120), and to the south a small animal room and storage space for a carpenter's bench, refrigerator, boxes, etc.

A space 4 feet in height, with concrete floor, lies beneath the rest of the building, whereby access can readily be gained to all drains, etc. beneath the ground floor.

*General arrangement.* To economize space, and to have as many research room windows as practicable fronting north whilst keeping the rooms adjacent to each other, the entrances are placed at both ends of the building. Two staircases are provided for safety in case of fire, and a straight corridor runs midway along the length of the building on two floors. There are eight research rooms occupying the ground floor and first floor, these rooms accommodating eight to sixteen workers.

The *main entrance* is to the east through double doors whose upper panels are glazed and guarded by a grill. The vestibule contains a commemorative tablet of bronze in a stone setting of appropriate design (see Fig. 5), whilst a small telephone chamber is situated at the bottom of the staircase shaft.

The *corridors* (ground floor and first floor) are cut off from the vestibules at each end by double swing-doors with glazed panels, being well lit by day through borrowed lights and transoms at their sides and from their ends by the light entering the vestibules through doors and windows.

Near the western staircase on all floors a space has been used to advantage by erecting light partition walls enclosing store-cupboards and closets for housemaids' sinks where brooms, pails, etc. can be kept. On the ground floor the sink and attendants' lavatory, etc., occupy but one space.

In the western vestibules on three floors there are *hoist holes* provided with teak trapdoors through which heavy articles can be raised from the basement to the top floor by means of a chain and pulley. This simple arrangement

functions in place of a lift whilst not cramping the floor space when out of use.

The *ground floor*, on the south side, contains cloak rooms and lavatories for both sexes, an office, a small waiting room for visitors, an incubator room, a laboratory assistants' room, a washing-up and sterilizing room. A photomicrographic room and four research rooms occupy the north side. The photographic room and adjoining dark room are each supplied with a radiator so that they are comfortably warm in winter and always free from damp. Through vents leading respectively from the ceiling of the dark room to the roof and from the photographic room to the hall these rooms are satisfactorily ventilated

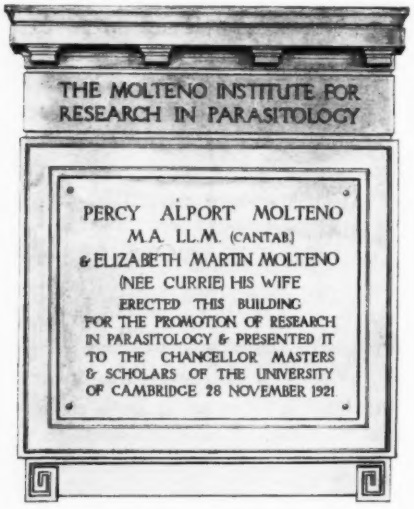

THE MOLTENO INSTITUTE FOR
RESEARCH IN PARASITOLOGY
PERCY ALPORT MOLTENO
M.A. LL.M. (CANTAB)
& ELIZABETH MARTIN MOLTENO
(NEE CURRIE) HIS WIFE
ERECTED THIS BUILDING
FOR THE PROMOTION OF RESEARCH
IN PARASITOLOGY & PRESENTED IT
TO THE CHANCELLOR MASTERS
& SCHOLARS OF THE UNIVERSITY
OF CAMBRIDGE 28 NOVEMBER 1921

Fig. 5. The commemorative tablet in the vestibule of the Institute. The tablet being of bronze and made to fit the stone setting with its incised and gilded inscription above. Designed by Mr Harry Redfern, F.R.I.B.A., the architect. The figure has been prepared from a retouched photograph.

whilst trapped against light, the air entering from the outside, as elsewhere, near the radiators.

The *first floor*, on the south side, contains a tea and rest room, a library, a lavatory, a laboratory assistants' room and chemical room. Four research rooms and an aquarium room occupy the north side.

The *tea and rest room* is regarded by the writer as a most useful feature in an institution of this kind. It serves several purposes: (*a*) as a gathering place for sociable intercourse among the workers at the Institute during the short interval when tea is provided, (*b*) as a place where those who may bring a meal with them can retire when they desire, (*c*) as a room where workers may rest or spend the night should this be necessary in connection with their researches. The room, in its arrangement and furniture, has nothing reminiscent of a

laboratory about it; being provided with comfortable chairs, a fire-place, a cupboard and hidden sink for storage and the washing up of eating utensils which are kept out of the laboratory entirely. A long, cushioned, bench which can be widened by a flap affords if need be a sleeping place; the writer has in the past spent many an uncomfortable night in laboratories that lacked such a resting place for workers who have to make periodic observations at night in connection with their researches.

The *aquarium room*, as shown in the plan, is on the first floor and it faces north[1]. It has a slate window bench that is drained by a white glazed channel. The asphalted floor slopes to one corner where there is a large drain to prevent the danger of flooding. The sink is large and shallow to facilitate the cleansing of large glass vessels which may be used as aquaria. Three stopcocks deliver tap-water to one side of the sink, one of them being fitted with a hose coupling. The rain-water supply to the aquarium flows down vertically through a glazed pipe from the slated collecting area on the roof (see below) and is stored in a slate cistern (position indicated on the plan by a dotted line), held in a steel frame beneath the ceiling of the aquarium room. The cistern measures $8' \times 4'\ 6'' \times 2'$[2], its capacity being about 350 gallons. The top of the cistern is covered with slate and access thereto is gained through a teak trapdoor in the floor of the room above, a movable slate slab preventing the entry of dust into the cistern. To obviate undue condensation of moisture upon the steel bearers and slate surface of the cistern in the room, the whole is enclosed in sheets of uralite with an interposed air-space. The water used for the aquaria is conducted out of the cistern in a tin pipe provided with two tinned stop-cocks with tapered nozzles, one over the sink, the other over the end of the window-bench nearest the sink, a glass gauge joined to the tin delivery-pipe near the cistern serving to indicate the stored water level. A vulcanite stand-pipe conducts any overflow from the cistern into a large pipe opening near the floor drain above-mentioned.

The *second floor* is almost entirely devoted to the research museum whose north side may serve for demonstrations, practical instruction, or for research work, being, if necessary, divided up by light movable partitions to form cubicles. Museum cases, cabinets and various cupboards occupy the south side. A preparation room opens into the museum at one end, whilst the northwest corner of the building contains a store-room.

The *roof*, to which access is gained at the west end, is flat and of reinforced concrete finished with asphalt, with a closed brick parapet, 4 feet high, forming a court in which there can be accommodated terraria, aquaria, and small animals in hutches, etc. Extending along the middle of the roof is the research museum skylight, constructed on the weaver-shed principle, glazed on the north and slated on the south. A glazed earthenware gutter collects the rain-

[1] The writer is much indebted to his friend Mr Edward Bles, M.A., for advice in practical matters relating to the arrangement of the aquarium room and its rain-water supply.

[2] See footnote, p. 121.

water from the whole length of this slated portion and voids it down the vertical pipe to the slate cistern in the aquarium room. At the west end of the roof is a hatchway to a vertical *chute* leading down to a closed space opening with a door near the furnace in the basement; this chute, finished in smooth concrete internally, serves for throwing down refuse from the top to the bottom of the building where it can be incinerated or otherwise dealt with.

The *stairs* outside the building are of stone; those within are granolithic with powdered carburundum (non-slip) finish, they measure 3′ 5″ in width. The bannisters are of iron painted dull black. The *internal surface of the walls* is lime-washed in the basements, plastered and white, cream, or otherwise distempered throughout, except in the photographic room and dark room which are painted black overall; in the lavatories the walls are coated with white enamel paint to a height of 5 feet above the floor. The *skirtings* are of concrete and usually 3 inches high, being mostly blackened, the concrete being preferred to wood. The *floors* are of concrete, partly reinforced, their surfaces being covered by red tiles in the vestibules, corridors and lavatories, black tiles and stone covering an area about the fireplace in the tea room; otherwise the floors are finished in Portland cement trowelled smooth, or asphalted (as on the roof) in the chemical, aquarium, sterilizing and dark rooms; a few of the rooms have the floors covered by dark green linoleum similar to that on the work benches; as linoleum is very expensive its use has necessarily been (we hope temporarily) restricted. *Woodwork.* The external doors and gate to cycle basement, window frames and ledges, and trap-doors to hoist are of teak; a few window ledges are of slate. The woodwork of the internal doors, borrowed lights, etc., is white enamelled throughout except in the basements; the *doors*, where not glazed, are smooth, unpanelled, consisting of a frame covered with boards of three-ply wood; three pairs of research rooms intercommunicate by sliding doors conveniently placed. The woodwork in the tea room and library (shelves 10″ deep) are of teak. Appropriate legends and numbers are painted in black on the doors. *Windows.* The frames and casements of the seven research rooms and aquarium (ground and first floors) are of steel; the central large fixed casement holding a single sheet of plate glass as in shop windows, the two casements flanking the central one being arranged to open so that their upper portion swings horizontally, the top edge falling inward, whilst the lower portion is hung vertically swinging one-third in and two-thirds out whereby they are readily cleaned; the lower sections of the flanking windows open in opposite ways so as to secure suitable ventilation according to the direction of the wind. The windows on the north side of the research museum, consisting of four lights each, have their lateral casements movable like those in the research rooms, the casements being of steel set in teak frames. The remaining windows of the building are leaded, the steel casements being set in teak frames. In all cases the upper line of the glazed portion of the window runs at a distance of about 6 inches from the ceiling whereby the rooms are brightened by the large amount of reflection from the ceiling.

*Work benches* extend across the width of the rooms and for a short distance to one side in the form of an L, being supported on steel T-bars set in the outer wall in cement. The tops are covered with green linoleum glued down to the thick deal boards beneath and all are edged with teak having rounded edges. The teak border on the free side nearest the worker is slightly broader than the thickness of the bench, the bottom margin thus affording a drip-edge in case fluids are spilled on the bench. The short arm of the L-shaped bench serves for the reception of an incubator, embedding bath, or the like. The benches are provided with electric light plugs and gas fittings conveniently placed so as to be as much as possible out of the way.

The *sinks* are white glazed earthenware throughout. Measured on the inside, those in the research rooms are 1′ 9″ × 1′ 4″ by 6″ in depth[1]; those in the sterilizing room (9″ deep) and photographic room (6″ deep) measure 2′ 4″ × 1′ 5″; that in the aquarium room 3′ 4″ × 1′ 9″ by 5″ in depth. Tap-nozzles are usually placed 14″ above the bottoms of sinks. As shown in the plans, the research room sinks and similar sinks elsewhere are each provided with a teak draining board and adjacent stone shelf, each measuring 2′ × 1′ 6″. The sinks empty into 3″ glazed drains, whose large callibre precludes stoppages if larger objects escape into the drains from the sinks. A considerable economy was effected by placing sinks on opposite sides of a wall so that they empty into a common downfall drain, such paired sinks and their accompanying draining boards and stone shelves being supported by but one set of T-steel rods which transfix the wall.

*Metal fittings.* There is little to note regarding these, but it may be mentioned that gun-metal has been used in place of brass wherever possible so as to save unnecessary labour in cleaning. Most of the door handles are of the "push, pull and turn" pattern and therefore specially to be commended for laboratory purposes.

*Some measurements relating to the building.*

The following measurements are noted since some of them may be of use as a guide to others who contemplate constructing laboratories: Externally *the building* measures 92′ × 44′ and 35′ in height to the top of the stone coping. The *corridors* are 6′ wide. The four *research rooms* on the ground floor and the corresponding rooms above measure 14′ in depth, the length of the middle pair being 15′ 6″, that of the other two being 15′ 10″. The *photographic room* (designed for a Zeiss optical bench) and the adjacent dark room are 16′ deep and have a width of 4′ 9″ and 5′ 6″ respectively, being separated by a light partition wall of hollow bricks. The corresponding small research room at the N.W. corner of the floor above measures 10′ 6″ in width. On the ground and first floors, south side, the rooms are 14′ deep except for the tea room which has a depth of 16′; the widths of these rooms being as follows: On the ground floor: *Sterilizing and Laboratory Assistants' room* 15′ 10″ and 15′ 6″ respectively, *Incubator room* 6′ 6″, *Waiting room* 7′ 7″, *Office* 12′ 3″; on the first floor: *Chemical room* 15′ 10″, *Laboratory Assistants' room* 11′ 9″, *Library* 26′ 10″, *Tea room* 15′ 9″. On the second floor, the *Research museum* measures 65′ × 36′, and both the preparation and store rooms measure 10′ 6″ × 16′. The size of the basements is indicated on p. 117. The

[1] The signs ′ and ″ denote feet and inches respectively.

basements are 6′ 9″ high, the ground and first floor rooms 10′ high, the second floor rooms 9′ high. Where there are no basements, the ground floor is suspended 4′ above the concreted surface of the ground-level. The *roof parapet* is 4′ high, the chimneys being but slightly higher. The *skylight* is 65′ long and consists of 34 lights (4′ × 2′) framed in teak, the glazing being double with a closed air-space between the pairs of panes; the *slated surface* which serves for the collection of rain-water measures 66′ 8″ × 7′ (area 467′) and is tilted at an angle of 30°, whilst the glazed surface is 4′ wide and stands at an angle of 60°. The internal measurement of the *chute* is 2′ × 2′, that of the *hoist-hole* 4′ × 4′.

The *work benches* throughout are 27″ wide, their surface being 33″ above floor-level. The *slate bench in the aquarium* window is 30″ wide and 21″ above floor-level. The *chemical bench* in the centre of the room measures 7′ × 4′. The *doors* measure 6′ 7″ × 3′ as a rule. The *windows* in seven research rooms and aquarium occupy almost the whole north side of the room, the fixed central pane measuring 5′ 11″ × 5′ 9″. The *borrowed lights* (3′ 4″ × 22″) are placed 6′ 11″ above floor-level, fifteen borrowed lights being on the ground floor and nine on the first floor, occurring either as transoms over doors or fixed in corridor walls into which they mostly open.

*Heating, Ventilation and Lighting.* The building is heated by hot water on the low pressure system, the boiler ("Coronation") being situated in the basement alongside the coal cellars. There are 44 radiators placed in rooms, corridors and landings, 18 being on the ground floor, 14 on the first floor, and 12 on the second floor. The radiators are mostly placed near windows beneath work benches but to one side so as not to incommode persons working at the bench; they draw fresh air through apertures from the outside and the warmed air passes up through a cast-iron grating in the bench beside the window. The radiators have been found to heat the building very efficiently. There are three open fireplaces in the building, two with modern gas hearths (in library and tea room), and one in the office where it is at times convenient to be able to burn papers. Apart from these sources of heat, arrangement was made whereby gas-stoves may be introduced into the building at some future period if required. For this purpose, small triangular gas-fume flues were built in eleven rooms by means of flat bricks, measuring 9″ × 9″, diagonally placed across one corner of the room, these flues leading up to the roof alongside the columns in the research museum; the small chimney-like vents to these flues are shown at five points on the plan of the roof (Fig. 4). The corner position to be occupied by gas-stoves, if required, is indicated on the plans. To instal gas-stoves it is merely necessary to cut a hole through the plaster and thin brick for the purpose of inserting the stove-pipe.

Ventilation is secured by opening windows, transoms, or borrowed lights, and by allowing the air to enter from the outside through the apertures near the radiators. Reference has already been made to the character of the windows (see p. 120).

Owing to the large windows, glazed tops of swing-doors at the ends of corridors, borrowed lights suitably placed, and to the general whiteness of the interior of the building, the latter appears singularly well illuminated during the daytime. Thoroughly efficient artificial illumination is secured by means of electric light distributed in the form of drop-lights, wall-brackets and wall-

plugs serving table lamps where they are most useful whilst having regard to economy.

It will suffice to mention that each research room is provided with (*a*) a central drop-light that can be moved up and down above the writing table, (*b*) a bracket-light above the sink, (*c*) a bracket-light above the short arm of the L-shaped bench used for the embedding bath, etc., (*d*) two plugs to table lamps on the work bench, these supplying two or four lamps as required. The bracket-lights are placed at a height of about 3 feet above the bench or sink. The drop-lights are ½-watt, 60-candle power, the others 30 c.p. throughout; the corridors are lit by 30 c.p. fixed drop-lights, corresponding lights in the research museum being 60 c.p. The wiring is all carried in flattened lead pipes attached to wooden strips, the pipes being protected by iron guards where liable to injury, this method of wiring having various advantages over that in which iron pipes are used for carrying the insulated wires.

Electric power plugs have been placed in five situations: the sterilizing room, chemical and photographic rooms and research museum.

*Equipment.* The Institute is well provided with all requisite apparatus including modern appliances for the study of the biology of parasites. Special attention is being given to securing facilities for the study of the best and most recent methods of conducting research in parasitology.

## SCIENTIFIC COLLECTIONS.

The collections of the Institute comprise numerous specimens acquired by the writer during many years, others presented to the Quick Laboratory and more recently to the Molteno Institute. The collections are intended primarily to aid the workers at the Institute and are housed in the research museum, the latter affording space for the considerable expansion of the collections which is expected in the future.

The collection of Ixodoidea, which is the most valuable at present, is one of the largest existing, besides being rich in types. There are many specimens of blood-sucking and parasitic insects and acari. The helminthological collection is rapidly growing in value, and, like the preceding, comprises types. Protozoological and mycological specimens are being steadily acquired, and there is a bacteriological cabinet. We hope to augment our collections by means of exchanges and through the further generosity of donors in different parts of the world.

A considerable amount of illustrative material, largely original, including diagrams prepared for the purpose of instruction in parasitology, is already contained in our museum.

*Portraits of scientific men.* A collection of about 300 portraits of those who have distinguished themselves in the domain of parasitology has been gathered by the writer and presented to the Institute. The portraits are mostly framed and hung chiefly in the well-lit corridors, the grouping being by nations and as far as possible by subjects. A number of these portraits are being published

in the form of a series appearing in *Parasitology* with accompanying biographical notes. The collection is of considerable interest to students of parasitology and others.

### The Library.

The basis of a departmental library has been formed by the gift to the Institute of the whole of the writer's scientific books, brochures, reports, journals and some thousands of reprints which are being suitably classified, bound and catalogued, new publications being continually added. Gifts and exchanges are also helping on the library.

The nucleus of a *Library Fund* has been formed through a benefaction received from Mrs Stella Churchill in memory of her late brother Dr Walter Myers, who died in Pará, Brazil in 1901 whilst investigating yellow fever[1].

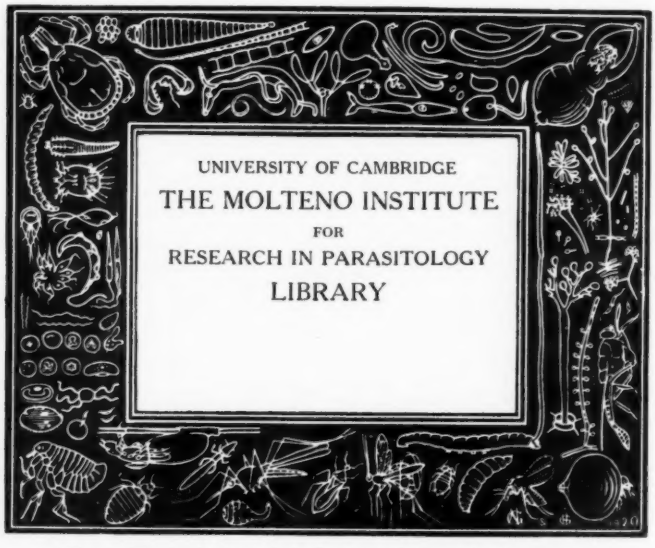



Fig. 6. The book-plate of the Institute designed by the writer.

The accompanying figure (Fig. 6) illustrates the book-plate designed by the writer for the library. The heavily parasitized border shows a reckless disregard for the relative size of the parasites depicted, most of the forms figured being readily recognizable to the initiated.

### Facilities for Publication.

The publication of the scientific work carried out at the Institute is greatly facilitated by the circumstance that the writer is the founder and editor of the two journals, *Parasitology* and *The Journal of Hygiene*, the first having now attained its 14th and the second its 21st volume. Both journals are

[1] For biography and portrait, see *Journal of Hygiene*, 1901, I. pp. 285–287.

published by the University Press, Cambridge. *Parasitology* first appeared as a Supplement to *The Journal of Hygiene* in March, 1908, but, commencing with the sixth volume (1913) it became an independent journal, and to-day it represents the leading periodical publication dealing with parasitology.

## PLANS FOR THE FUTURE DEVELOPMENT OF THE INSTITUTE AND THEIR DEPENDENCE ON FURTHER ENDOWMENT.

The Institute was founded for the advancement of our knowledge of Parasitology in all its branches, being in this respect the first of its kind. Hitherto Parasitology has been taught in a limited way in professional schools, either medical or veterinary, in zoological and botanical laboratories, or in conjunction with agriculture and fisheries; consequently the student has been precluded from obtaining a general survey of the subject as a science. Similarly, in the matter of research, the work carried on in the various schools has been largely confined to problems having only a practical professional bearing. The Molteno Institute proposes to deal with Parasitology on a broad biological basis, the research and instruction offered therein being directed both to purely scientific and practical problems because pure and applied science are inseparably interwoven and many of the most important practical discoveries in the past have had their origin in purely scientific investigation.

Parasites and parasitic affections are widely distributed in Nature, the chief forms among the innumerable parasites affecting animals and plants being found among Protozoa, Vermes, Insecta, Acarina, and Fungi including Bacteria. It is evident therefore that the student desiring to obtain a broad survey of Parasitology will require to familiarize himself with a large number of widely divergent groups of organisms and that he should have corresponding facilities for their study placed at his disposal.

The well-equipped Institute herein described is an instrument of research which cannot be used to full advantage without ample funds. To render the work of the Institute efficient and to carry out the plan which governed its design and equipment it is necessary that an endowment fund or funds shall be established.

The present permanent endowments yield a total annual income of £861 derived from (*a*) the Quick Fund (£300 for research and laboratory), (*b*) the Molteno Benefaction (£546 for maintenance of Institute), and (*c*) the Walter Myers Fund (£5 for Library). Of this amount £500 go to meet the exorbitant rates and taxes at present demanded on the building, leaving but £351 for general purposes. Needless to say this sum represents but a fraction of the annual expenditure required to run the Institute and pay stipends, salaries, maintenance, cost of research, apparatus, chemicals, books, etc.

The main expenditure in running the Institute is met by grants for research derived from various sources as in the case of the Quick Laboratory during previous years. It will be readily understood that it is a grave drawback to any Research Institution to be dependent on grants because these are

necessarily obtained at irregular intervals and for specified purposes. Under the most favourable conditions, grants are but made from year to year, a circumstance that introduces a distracting element of uncertainty into the policy of the Institute. Moreover, since grants can only be obtained, as a rule, for specific researches that appeal to the judgment of the grantors, a most undesirable limitation is placed upon the Institution in its scientific work. Means should therefore be found in the near future to obtain funds wherewith scientific work may be conducted in a more unfettered manner.

In connection with the Institute, the position of *Parasitology* requires consideration. Founded in 1911 by the writer, this Journal has been carried on by him at a heavy personal loss during most of the years of its existence (1911–21). It is hardly to be expected that a publication of this kind should be self-supporting, essential though it be for the coordination and development of research, its circulation being necessarily limited, but it is clear that the cost of maintenance is small in proportion to its usefulness. It would be well if the Journal were made the official organ for the publication of the work done by investigators at the Institute whilst still serving for the presentation of papers derived from other sources. A suitable sum should therefore be made available toward the support of this Journal from endowments which may accrue to the Institute in the future, for, in view of the continued loss in publication, its continued existence is at stake.

It is hoped, therefore, that in the near future adequate funds will be found for the permanent endowment of the Institute so that it may develope as it should and perform the functions for which it is intended.

ACKNOWLEDGMENTS.

In concluding, the writer would express his deep sense of gratitude to Mr and Mrs Percy Alport Molteno for the splendid gift they have made to Science, the Empire and the University, a gift which will be appreciated to a growing degree in the future. Our great indebtedness to the late Mr Frederick James Quick, founder of the Quick Professorship of Biology, should be acknowledged anew, for, thanks to his foresight and the provisions of his legacy, wisely carried out by his Trustees and the Managers of the Quick Fund, the means provided by both the Molteno and Quick benefactions serve one and the same excellent end. We are, moreover, under great obligations to those public bodies and private persons who have helped on our work in the past (see p. 104) and, more recently, especially to the late Lord Strathcona and Mount Royal for his benefaction (see p. 108).

Our warmest thanks are due to Mr Harry Redfern, F.R.I.B.A., the architect of the Institute, for the extremely able manner in which he designed and carried out the building plans and for his ever friendly consideration of our wishes. The good work of the builders, Messrs William Saint and Son of Cambridge, speaks for itself, and we are grateful to their excellent foreman Mr Brain for the painstaking manner in which he carried out his multifarious duties.

# THE DEVELOPMENT OF *HELIGMOSOMUM MURIS* YOKOGAWA, A NEMATODE FROM THE INTESTINE OF THE WILD RAT[1].

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(With Plates VII—XII and 8 Text-figures.)

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## I. INTRODUCTION.

The post-embryonic development of nematodes is very insufficiently known. A surprisingly small number of forms have been studied and in many of these investigations the work is entirely inadequate. Leuckart (1887) investigated

[1] This paper is a contribution from the Department of Medical Zoology of the School of Hygiene and Public Health of the Johns Hopkins University.

the post-embryonal stages of *Allantnema mirabile* and Neuhaus (1903) studied these stages in a free-living nematode, *Rhabditis nigrovenosa*. The most notable study on the post-embryonal development of a nematode was made by Looss (1897, 1911) on the hookworm, *Ancylostoma duodenale*. More recently in South Africa Veglia (1915) has made extensive studies on the post-embryonal development of *Haemonchus contortus* from the sheep, and Theiler and Robertson (1915) have investigated these stages in *Trichostrongylus douglasi*, the wireworm from the ostrich. In the studies which have been made of the post-embryonal development of the Strongylidae the free-living stages, especially of the hookworms, have been very completely investigated. While in only a comparatively few forms have the free-living stages been studied in detail, there is found to be a considerable degree of uniformity in the development and relationship of these stages, so that we have an adequate conception of what the stages of development of this stage are. It is entirely otherwise with the parasitic development in this family. The literature gives an entirely inadequate conception of the morphogenesis of the various organ systems, and on some phases of this development there is no information whatsoever. This lack of knowledge is probably partly due to the fact that in most nematodes this period is of considerable length and many of the hosts studied are large animals.

*Heligmosomum muris*, which I described from the rat (Yokogawa, 1920), proved to be remarkably good material for the study of development during the parasitic stages. This form is small and develops in ordinary culture rats as well as in wild rats. But best of all infection can be easily obtained and the development in the rat requires only a few days. This made it possible to obtain an abundance of material of the stages of development and to obtain at any time material of any particular stage on which further observations were needed.

All the observations recorded in this paper were made from living specimens. To quiet the larvae the slide could be heated or exposed to direct sunlight. To find the larvae in the lungs of the experimental rats it was necessary to tease the tissue into very small pieces in normal salt solution. These pieces were then carefully crushed in a mortar and filtered through a fine wire screen. The filtrate was then centrifuged and the larvae if present would be recovered. After the larvae had made their way to the intestine it was not difficult to pick them from the surface of the mucous membrane.

In the present paper no attempt is made to study in detail the embryonic development which many authors have studied in nematodes. While the free-living larval stages were studied as fully as the time would permit no attempt has been made to discuss critically these stages for the Strongylidae. Looss (1911) gives a very complete and critical analysis of these stages in *Ancylostoma duodenale*. The main emphasis in the paper is placed on the study of the parasitic development, and especially on the development of the reproductive organs.

## II. THE FREE-LIVING LARVAL STAGES.

### 1. DEVELOPMENT OF THE EGG.

#### (*a*) *Morphology of the Egg.*

The eggs of *Heligmosomum muris* are ellipsoidal in shape and have a very thin shell. The average size is 0·05824 mm. by 0·03276 mm.; a minimum size is 0·0546 mm. by 0·0309 mm. and a maximum is 0·06188 mm. by 0·03458 mm. Segmentation of the egg begins within the uterus of the female. Eggs in the one-cell stage are found in the upper part of the uterus, while in the lower part of the uterus they are in the 4 to 16 cell stages. In fresh faeces, the embryo is found most frequently in the 16 to 20 blastomere stage, while eggs which have just been given off by the female are usually in the 4 to 16 cell stages. Exceptionally, eggs may develop to the morula stage in the intestine of the host but they are usually found in earlier stages.

#### (*b*) *Formation and Hatching of the Embryo.*

The embryonic development of the larva and the hatching of the egg of *Heligmosomum muris* are very similar to these stages as described for other members of the family Strongylidae, therefore I will include only a brief outline of these phases of development.

For the observation of the embryonic development, I placed eggs which had just escaped from the female in a liquid culture. These experiments were carried out in the beginning of the summer of 1920 in Baltimore, at temperatures favourable for the development. The period of embryonic development varies according to the temperature and the media in which the eggs are placed. The following notes are the summary of the observations from these experiments. In 4 to 6 hours after placing the eggs in the culture a large number of them were found in the morula stage and some even in the advanced morula stage.

In 8 to 10 hours the majority of the eggs had reached the "tadpole" stage, and some already showed a few structural details. At this stage the anterior end is broader than the posterior and somewhat conical and the cylindrical, buccal-cavity is visible. The beginning of the oesophagus and the intestine can be seen as a strand of dark cells.

After 12 to 15 hours many of the eggs were in the advanced "tadpole" stage, while others already contained the rhabditiform larva. In some cases the embryo had attained three times the length of the egg, and in a few of the eggs it was four times this length. The shape of the body of the larva is cylindrical, the head is conical, and the tail is long. The mouth cavity shows clearly in optical section as two longitudinal lines, each terminating posteriorly in a point. The rhabditiform oesophagus and the chyle intestine are also well-developed. At this period a few free larvae are occasionally found already hatched.

In 17 to 20 hours about 20 per cent. of the eggs are found already hatched and the majority of eggs seem to hatch between 20 and 24 hours.

## 2. Development of the Larvae in the Free-living Stage.

### (*a*) *Method of Culture.*

In my studies of the formation of the embryo and the free development of the larvae I made many cultures of the faeces of wild rats infested with *Heligmosomum muris*. I found that cultures made in liquid media are best for the study of the formation of the embryo and the earlier stages of larval development, while those made in solid media are most suitable for the study of the development of the later larval stages.

The best results with cultures in liquid media were obtained by using a filtered decoction of faeces prepared in the following manner. One teaspoonful of normal faeces from white rats was boiled in 100 c.c. of tap water. The mixture was then filtered, and the decoction poured into a glass dish in a very thin layer. To this were added many eggs fresh from the females. The glass dish was then kept at room temperature, since this work was carried on in the summer time and was covered to prevent evaporation. For the purpose of examining the progress of development the dish can be placed from time to time under the low power of a microscope. In this way the hatching of the egg or any of the developmental stages can easily be observed on a number of larvae at the same time. By means of a pipette the larvae can be picked out, transferred to a drop of water on a glass slide and examined under high power. This method of cultivation is very convenient for the studying of the early stages of larval development. It is not suited, however, for the study of the development of the infective larvae, since the majority of the larvae cannot complete the first moult in liquid media.

The method of making the cultures of solid media was very simple. Fresh faeces from rats infected with *H. muris* was smeared on moist filter paper in a covered dish. This culture must be kept moist and the faeces must be spread out well on the filter paper to give sufficient air. It is not necessary, however, to add charcoal to avoid fermentation as in the cultures of human faeces containing hookworm eggs. The mature infective larvae appear on the filter paper or on the walls of the dish four to five days after the making of the culture. They are later found in great numbers along the edge of the filter paper giving the appearance of minute threads.

### (*b*) *A General Description of the Stages of the Post-embryonal Development.*

In the literature on the development of nematodes the statement is made that four moults are necessary for the complete development. Looss (1911) makes this definite statement: "the number of the moults in the case of the nematodes is apparently always four. It remains to be seen whether further experience will confirm or overthrow this apparent rule." In the case of *H. muris* only three moults were observed. Early in my work I was struck with the fact that I could find only one moult in the free-living stage and suspected that I had overlooked the first moult. After repeated examina-

tions of the free development of the larvae I finally became convinced that there was only one moult. Finally the finding of the double layers of the cuticula in the adult stage struck me as important in this connection. The separation of the outer cuticula at this stage goes on just as if the worm were preparing for a moult but it remains always attached. It is only a short time after the completion of the third moult that the double conditions of the cuticula develops, and the space between the two layers of cuticula gradually becomes larger. The outer cuticula of the female is much looser than that of the male and extends posteriorly, forming a peculiar sac (Yokogawa, 1920). The outer cuticula is thick and has the transverse striations limited to the prominent longitudinal ridges, while the inner one is thinner and has only the transverse striations. No other case of a double cuticula has been found recorded for nematodes. It is probable that this condition is a characteristic of the genus *Heligmosomum*, which has escaped notice in the other species that have been described. This condition undoubtedly represents an incomplete moult. Therefore it seems to me that we can safely conclude that in *H. muris* the condition is the same as in other nematodes but that the second moult is transferred into the parasitic life and the fourth is never completed.

Looss (1911) divided the post-embryonal development of the nematodes into five periods which are separated by four moults. This method of division is commonly used. This division does not hold good for *H. muris*, since if in this form the stages were separated by the moults the development would include only four stages divided by three moults, the second stage including both a free and a parasitic stage and two distinct periods of development. In this case, it seems to be necessary to consider as a separate stage the time from the entrance into the final host to the second moult. This stage is then the third stage or the first parasitic stage and is separated from the second stage by the penetration of the larvae through the skin.

The post-embryonal development of *Heligmosomum muris* is divided into five stages by three moults. The first two stages are passed outside the host, as free-living larvae, and are separated by a relatively long moulting period, in which there are many structural changes. There exists some difference of opinion in regard to exactly when the second larval stage in the free life of nematodes commences. Previous authors have described the second stage as beginning after the larva has completed its first moult. From the biological point of view larvae are already in the second stage when the structural changes which go on during the moult have taken place. In the case of *H. muris*, the duration of the first moult is relatively long and remarkable structural changes occur during this period. Since it seems necessary for the purposes of description to establish a definite line of demarcation between the first and the second stages, I will here describe as a part of the first stage those changes which occur up to the completion of the first moult.

The three last stages are passed inside the host. The third larval stage or the first parasitic stage is separated from the second larval stage not by a

moult as in the hookworm and other forms but by the penetration of the larvae through the skin of the host. Entering the fifth stage the worm is sexually mature and is usually spoken of as the adult worm.

### (c) *The First Larval Stage.*

In this stage, which extends from the hatching of the eggs to the first moult, the growth and development of the larvae are very remarkable. The changes were so great that it seemed probable that this stage must be passed without the lethargic stage which has been described for the larvae of other Strongylidae. Repeated examinations failed to show a lethargic stage so that the conclusion was reached that the first stage in the development of *H. muris* was passed in continuous development and activity.

I will now describe the structure of the larvae in the first stage of development.

*Size of the larvae.* The larvae (Fig. 1, Plate VII) hatched under natural conditions vary from 0·28 mm. to 0·30 mm. in length and from 0·015 mm. to 0·018 mm. in thickness, measured just behind the base of the oesophagus. They gradually grow until the time of the first moult, when they measure from 0·68 mm. to 0·78 mm. in length and from 0·032 mm. to 0·036 mm. in thickness. The larvae at this stage (Figs. 2, 3) belong to the rhabditiform type. The form of the body is cylindrical, decreasing in thickness from the base of the oesophagus to the tail. The tail is extremely slender, ending in a hair-like point.

*Body-cavity.* In the larva just hatched from the egg the body-cavity is very small, consisting of a slight space around the digestive tract. Anteriorly the body-cavity is slightly expanded around the anterior part of the buccal-cavity and surrounds the digestive tract to the region of the anus (Fig. 2). Towards the end of the first larval stage this space is almost obliterated by the expansion of the chyle intestine. The lateral and the ventral and dorsal bands cannot be distinguished at this stage.

*Cuticula.* The cuticula of the newly hatched larvae is very thin and without markings. The only change which it undergoes in the first stage is an increase in thickness as the size of the larva increases.

*Buccal-cavity.* The buccal-cavity is quite long, having a length of 0·012 mm. to 0·016 mm. and is cylindrical in shape.

*Oesophagus.* The oesophagus is rhabditoid in shape. The lumen appears as a clear line, and the "Y-shaped mark" in the centre of the bulb is quite clearly visible. The walls of the oesophagus are thick and transparent, containing some nuclei of muscle cells and have fine transverse striations. The length of the oesophagus varies from 0·06 mm. to 0·146 mm. according to the length of the larvae (see Table I).

*Chyle intestine.* The chyle intestine extends through the body from the oesophagus to the rectum. When observed from the side its lumen has a slightly irregular zigzag course. The wall of the intestine consists of two rows of eight cells, one row on the dorsal side and the other on the ventral side.

These cells are irregular flattened, cuboidal in shape, with oval nuclei. They jut into the lumen of the intestine reducing it to a mere line. The cells of the intestinal wall vary in size, even in the same specimen, according to their position, viz., the cells situated at the anterior and the posterior part of the intestine are much smaller than those in the middle region. The protoplasm of these cells contains fine granules which increase in number with the growth of the body. Accordingly the nuclei become difficult to see in the later development of the first larval stage. At the boundary line between the chyle intestine and the oesophagus are situated four cells (Fig. 2, *iv*, Plate VII), dorsally, two on each side, which represent the primordium of the intestinal valves. These cells are very small and clear and each contains a round nucleus.

*Rectum.* The rectum is a very fine slit-like canal lined by a thin chitinous membrane. Its length varies from 0·015 mm. to 0·055 mm. according to the length of the body. At the point where it joins the chyle intestine two to three small cells are visible, which seem to be the primordium of the rectal ligament (Fig. 2, *rc*). The rectum runs diagonally and is surrounded by a cell-group. The distance of the anus from the tip of the tail varies in the different sizes from 0·052 mm. to 0·11 mm. (see Table I).

*Nervous system.* At the constriction of the oesophagus of the youngest larva of the first stage there are found a large number of round cells surrounding the oesophagus. The majority of these cells belong to the nervous system. The nerve ring appears as a band surrounded by a number of these cells toward the end of this stage (Fig. 4, *n*, Plate VII).

*Excretory apparatus.* In the larvae just hatched from the eggs a number of round cells are found on the ventral side at the base of the oesophagus and at the anterior limit of the chyle intestine. This cell group is not at this stage sharply separated from the nerve cell group. In the last period of the first stage, two pear-shaped relatively large cells can be clearly seen at the same place occupied in the earlier stages by the cell-group mentioned above. These two cells are apparently separated from the nerve cell group, and are situated on the ventral side of the anterior part of the chyle intestine, with their narrow parts pointing anteriorly (Fig. 3, *cg*, Plate VII). In the front of these cells, a short canal is visible which enters into a group of cells. This canal is apparently the beginning of the excretory canal. The excretory pore cannot yet be distinguished.

*Genital primordium.* The germ anlage is recognizable as a small elongated body, measuring 0·006 mm. × 0·004 mm. to 0·01 mm. × 0·06 mm., according to the growth of the larvae (Figs. 1, 2 and 4, *gp*). In the youngest larvae it apparently consists of two cells. It is located on the ventral side between the chyle intestine and the body wall near the middle body.

Table I shows the increases in body length and in the length of certain other parts during the first stage of development.

Table I.

*Increases in Size of the Body of* H. muris *during the First Stage of Development.*

| Specimen number | Length (mm.) | Width (mm.) | Buccal-cavity (depth) (mm.) | Oesophagus (length) (mm.) | Tail (length) (mm.) |
|---|---|---|---|---|---|
| 1 | 0·28 | 0·015 | 0·014 | 0·072 | 0·052 |
| 2 | 0·300 | 0·018 | 0·012 | 0·060 | 0·06 |
| 3 | 0·395 | 0·018 | 0·013 | 0·080 | 0·08 |
| 4 | 0·419 | 0·022 | 0·013 | 0·086 | 0·09 |
| 5 | 0·442 | 0·022 | 0·013 | 0·110 | 0·09 |
| 6 | 0·560 | 0·031 | 0·014 | 0·123 | 0·10 |
| 7 | 0·640 | 0·030 | 0·0145 | 0·131 | 0·10 |
| 8 | 0·650 | 0·032 | 0·014 | 0·116 | 0·11 |
| 9 | 0·680 | 0·032 | 0·014 | 0·125 | 0·10 |
| 10 | 0·700 | 0·033 | 0·015 | 0·127 | 0·10 |
| 11 | 0·720 | 0·035 | 0·016 | 0·125 | 0·11 |

*Activity during first larval stage.* The newly hatched larvae are small and move very slowly. After a few hours they move more actively and commence to feed. In the larvae at this stage a contraction of the intestine can be noted, causing a bulging of its posterior end. During the second day, the growth of the larvae is remarkable and constant movements are noted. Usually about two days after hatching when the chyle intestine becomes packed with granules the movements become somewhat slower. After this they start in on the first moult.

### (*d*) *The First Moult.*

At the time of the beginning of the first moult, the chyle intestine appears to contain a great amount of refractive granular material. These granules are the globules of food material stored in the cells lining the intestine. These (Fig. 3, Plate VII) intestinal cells seem to be entering into a period of division, since many nuclei can be seen in them. This division of the cells proceeds from the anterior region backwards. Therefore the cells in the posterior region of the intestine at times will show no evidence of cell division, while in its anterior region this process is apparently going on. By this cell division, the cells lining the intestinal wall are modified into flattened cells containing fine yellowish brown pigment granules, and transparent ellipsoidal nuclei (Fig. 4). This cell division in the intestinal wall is a revolutionary process, since the cells do not increase in number. Those cells which jut into the lumen of the intestine break off after division and seem by degeneration to set free food material which is utilized during the moulting period. This revolutionary modification greatly increases the width of the intestinal lumen, which now loses its irregular zigzag character (Fig. 4, Plate VII).

During the first moult, the constriction of the oesophagus becomes less marked and it loses its rhabditoid shape. Also a newly formed cuticula gradually makes its appearance. After a while the tail becomes separated within the old cuticula and the beginnings of the lateral bands of the new cuticula appear (Fig. 5, Plate VIII). The newly formed tail is blunter and shorter than during

the former stage. Therefore, when these structural changes have been accomplished the larvae themselves have decreased considerably in length.

It is very difficult to determine exactly when the first moulting begins and when the sheathed larvae cast their old skins, since the structural changes proceed very slowly, and the ecdysis usually does not occur in liquid media. The casting of the old cuticula is a purely mechanical process and is effected by the activity of the larvae at the beginning of the second stage. The old cuticula, however, is so thick and rigid that the larvae cannot easily rid themselves of it without mechanical assistance. Accordingly the larvae after the completion of the structural changes described above prefer to penetrate into the filter paper or into pieces of faeces or to climb up the wall of the container in order to bring themselves in contact with some surface which will offer resistance. At this time the posterior end of the old cuticula usually becomes bent in the form of a hook (Fig. 5, Plate VIII). Occasionally a larva can be seen to be firmly attached by means of this hook to a piece of faeces, as it begins to free itself from the sheath.

In solid cultures, the structural changes of the larvae can be noted in 60 to 80 hours after the beginning of development, and some mature larvae (in the second stage) are found at the edge of the filter paper or on the sides of the container in 100 to 120 hours.

Measurements of the larvae toward the end of the moulting period show that while the length of the sheath is 0·77 mm. to 0·82 mm., the larvae within the sheaths are only 0·62 mm. to 0·75 mm. in length. In the moulting period, the movements of the larvae are slow and sometimes they are very quiet. They always react, however, to any stimulus. If they are removed from the culture into water about 5 mm. in depth, they will become quiet within several hours and finally die.

(*e*) *The Second Larval Stage.* (The infective stage.)

The larvae after the first moult are usually found at the edge of the filter paper or on the wall of the container. This stage is reached under favourable conditions five days after the cultures are made. Since the structural changes which occur during the first moult are very pronounced, the structure of the larvae during the second stage differs fundamentally from that of the first stage. Those larvae (Fig. 6, Plate VIII) are now ready to infect the host and differ from the larvae of other known Strongylidae in not having any sheath.

*Shape and size.* In shape, they do not differ greatly from the first stage except that the tail is short and blunt, having various shapes as shown in Text-fig. 4. These variations are nothing but individual differences. The larvae in this stage do not vary much in size, averaging 0·69 mm. by 0·027 mm.

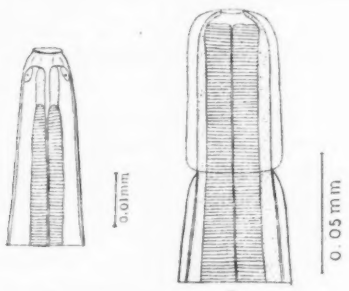
*Body-cavity.* The body-cavity is so narrow that it can only be detected with difficulty.

*The cuticula.* The cuticula shows faint transverse striations. On each side of the body there is a sharp narrow projection of the cuticula extending from

the region of the oesophagus to the posterior end. In the anterior region of the body three to four small highly refractile specks, like spines, are found on the surface of the cuticula at the region about the middle part of the oesophagus. Similar structures are recognizable in the tail region.

*Subcuticle and musculature.* It is difficult to understand the details of the structure of subcuticle and muscle layers in the optical sections of the living larvae. However, the lateral bands can be distinguished easily as two longitudinal strands at the sides of the body, since they are more transparent than the two neighbouring muscular areas. The dorsal and the ventral bands are not clearly distinguished.

*The buccal-cavity.* The buccal-cavity is narrower and shorter than in the larvae in the first stage. Its structure is shown in Text-fig. 1 *a*.




Text-fig. 1. Structures of anterior end. *a*, Mature free-living larva; *b*, adult.

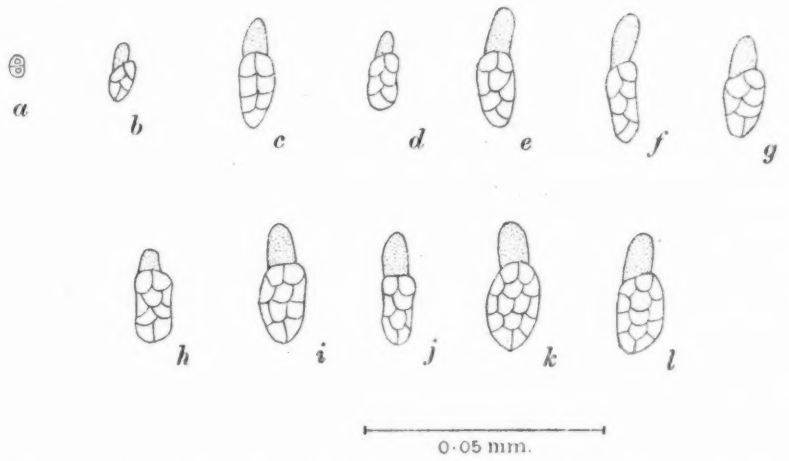
*Oesophagus.* The oesophagus is more or less claviform in shape and a little more slender than in the previous stage. Its lumen appears as a straight line. At the posterior end of the oesophagus there are three pairs of clear cells, each containing a vesicular nucleus (Fig. 6, *eg*, Plate VIII). These cells seem to correspond to the "oesophageal glands" described by Looss (1911) for the hookworm larva. They first become visible in larvae which have completed their metamorphosis.

*The intestine.* The intestinal lumen is very wide and contains a certain quantity of fine granules. The intestinal wall is composed as described above of two rows of eight flat cells, each containing an ellipsoidal nucleus. The protoplasm of these cells has increased somewhat in thickness over the condition just after the division of the cells. They have a uniform thickness along the whole length of the intestine. The nuclei in the cells are sometimes difficult to find, being covered by pigment granules.

*Nervous system.* The oesophageal ring is more clearly defined and has the same position as in the first stage. Details of the structure of the nervous system are difficult to make out in the living specimens.

*The excretory system.* In the mature larvae, the cervical glands become clearly recognizable by their large transparent ellipsoidal nuclei (Fig. 6, *ncg*,

Plate VIII). They are found in the dorso-lateral regions of the body. One of them is located at a distance of 0·06 to 0·08 mm. from the base of the oesophagus, and the other about the same distance behind the anterior one. These glands seem to have developed from the large pear-shaped cells, which were found in the first stage on the ventral side of the region where the oesophagus joins the intestine. The excretory pore opens at the ventral side at a distance of 0·13 mm. to 0·135 mm. from the anterior end of the body. Although the cervical gland-cells may be connected with the excretory pore at this stage, I could not trace any such connection clearly.




Text-fig. 2. Development of the genital primordium during the free-living stage and at the beginning of the first parasitic stage. *a*, From newly hatched larva; *b*, during the first moult; *c–h*, shapes assumed during the second larval stage; *i–l*, shapes assumed during the first part of the first parasitic stage, 15 hours after infection.

*The genital anlage.* The genital anlage (Fig. 6, *gp*, Plate VIII) is represented by an ellipsoidal or somewhat spindle-shaped transparent body which is situated ventrally in the region of the fourth or the fifth cells of the intestinal wall. Usually there can be seen beside the genital anlage a dark granular body as shown in the figures (Text-fig. 2). This body is so close to the genital anlage that it seems almost to be a part of it. I have, however, not succeeded in identifying this body in later development. The genital anlage consists of 6 to 8 cells and measures 0·0012 to 0·0017 mm. by 0·007 to 0·008 mm. It is impossible to distinguish the sexes at this stage.

Table II shows the size of the various parts of the larvae at this stage.

Table II.

*Measurements of Larvae of* H. muris *in the Infective Stage.*

| | Length (mm.) | Width (mm.) | Buccal-cavity (depth) (mm.) | Oesophagus (length) (mm.) | Position of excretory pore (from ant. end) | Tail (length) (mm.) |
|---|---|---|---|---|---|---|
| 18 days after culture (in faeces) | 0·680 | 0·028 | 0·0125 | 0·140 | 0·130 | 0·047 |
| | 0·715 | 0·026 | 0·0110 | 0·148 | 0·132 | 0·042 |
| | 0·745 | 0·026 | 0·0120 | 0·148 | 0·137 | 0·045 |
| | 0·630 | 0·025 | 0·0100 | 0·152 | 0·135 | 0·043 |
| | 0·760 | 0·030 | 0·011 | 0·154 | 0·132 | 0·050 |
| 14 days after culture (in faeces) | 0·652 | 0·026 | 0·011 | 0·129 | 0·134 | 0·044 |
| | 0·680 | 0·026 | 0·012 | 0·135 | 0·130 | 0·044 |
| | 0·712 | 0·027 | 0·012 | 0·148 | 0·132 | 0·046 |
| | 0·700 | 0·027 | 0·012 | 0·138 | 0·135 | 0·046 |
| | 0·65 | 0·027 | 0·011 | 0·130 | 0·132 | 0·044 |

*Activities of the mature or infective larvae.* The mature larvae usually are found along the edges of the filter paper, where they extend themselves in the air and wave back and forth slowly. They appear like minute hairs along the edge of the paper. If they are removed into water, they move actively as compared to the movement in the first stage. Their movement can best be described as "swimming." They are more resistant than the younger larvae to all the influences of the environment. They are, however, less resistant than the mature larvae of other Strongylidae which are enclosed in protective sheaths.

### 3. The Influence of the Environment on the Eggs and Larvae.

From my experience in culturing the larvae of *H. muris* I learned the following facts in regard to the effect of environment.

#### (*a*) *Air.*

The eggs of *Heligmosomum muris* require a certain amount of oxygen for their development since they do not develop beyond the morula stage in liquid media of more than 0·2 cm. in depth, while the eggs hatch and the larvae develop normally in liquid media of less than 1 mm. in depth.

I am of the opinion that more air is required during the development of eggs and larvae than for resting eggs and mature larvae, since the mature larvae were found alive for a long time even when kept in water at a depth of 1 cm. or more, while the developing larvae died under the same conditions in several hours to a few days according to the stage of their development.

#### (*b*) *Light.*

The development of the eggs and larvae of *H. muris* cultured in faeces does not seem to be influenced to any extent by diffused sunlight, although darkness appears to be the most suitable condition for development. If cultures containing mature larvae are examined after they have been kept for a considerable time in darkness and compared with cultures which have been kept for a period in the light, the cultures from the darkness will show a larger

number of larvae on the edges of the filter paper and these larvae will be more active.

On the contrary, if the larvae are exposed to direct sunlight, they soon become quiet and in a short time will be found to be dead. Further the eggs will not develop and hatch when the cultures are kept in direct sunlight. This relation to light is very interesting when we consider that the normal environment for the development of the larvae, and the place where they would most probably infect their hosts, would be in the dark burrows of the rats.

(*c*) *Moisture.*

I did not carry out any definite series of experiments to determine the most favourable degree of moisture or the resistance of the larvae to desiccation. It is evident, however, that some moisture is necessary for the development of the eggs and larvae of *H. muris*. I was able to observe that the eggs and larvae develop well under the condition of moisture, in which the filter paper used for culturing was kept about as moist as the faeces are at the time of defecation. If the faeces are soaked with water, the development often failed. On the contrary, if the cultures are not kept quite moist the larvae do not develop well.

The resistance of the larvae to desiccation varies according to the degree of their development. The mature larvae are more resistant than the other stages. They were found alive for a month or more on the walls of the covered containers in which the cultures were kept. They were also alive on a glass slide which was exposed in the air for more than two days. The young larvae were killed in dried cultures and on a glass slide in several hours.

(*d*) *Temperature.*

I have no definite experimental data to show what temperature is most suitable for the development of the eggs and larvae. My experience with culturing showed that the development was more rapid during the hot summer period than during the spring and autumn when the temperature was lower.

## III. METHOD OF INFECTION AND MIGRATION IN THE HOST.

After I had learned to culture infective larvae in quantity I tried two series of experiments on white rats to determine the method of infection with *H. muris*. In one series of experiments the mature larvae were fed to the rats and in the other they were brought into contact with their skin under conditions favourable for penetration.

### 1. INFECTION THROUGH THE MOUTH.

In this experiment seven tame rats were given great numbers of the mature larvae of *H. muris* on bread and watched carefully to make sure that they actually ingested the larvae. All of the rats were dissected at varying periods after the feedings and were found to contain only small numbers of the parasite, as summarized in Table III.

Table III.

*The Results of Feeding Rats with the Larvae of* H. muris.

| Date of feeding | Age of larvae (duration after culture) | Date of examination | Duration of infestation | Results |
|---|---|---|---|---|
| April 19 | 6 days | May 10 | 22 days | 4 adult females<br>3 adult males |
| May 21 | 10 days | June 13 | 23 days | 2 adult females<br>3 adult males |
| May 22 | 11 days | June 5 | 14 days | 2 adult females<br>2 adult males |
| May 22 | 11 days | June 5 | 14 days | 1 adult female<br>2 adult males |
| May 22 | 11 days | May 31 | 9 days | 3 adult females<br>1 adult male |
| May 24 | 13 days | June 6 | 13 days | None |
| May 24 | 13 days | May 25 | 1 day | None |

The above experiments show that when infective larvae are fed to rats only a small proportion are able to reach the intestine.

### 2. Infection through the Skin.

In the early experiments on infection through the skin the rats were always fastened in an aluminium form and the hair on the abdominal wall was cut very short. Then a large number of the mature larvae were put in water on the surface of the skin and the rats were kept in the shade until the water had dried. In the post-mortem examination the infestation was always found proportionate to the number of larvae applied. Later I found that the rats were infected very easily through the skin by applying the mature larvae to any part of the body. The present work was carried out by employing the simple method of application of the mature larvae to any parts of the skin of the rats after cutting the hair.

*Migratory course of the larvae in the final host.* The larvae placed on the skin of the rats penetrate very easily and quickly into the tissues and travel to the lungs, by means of blood-stream. Since the larvae were found in the trachea and reach the intestine soon after leaving the lungs it seems evident that they penetrate into the air sacs of the lungs and make their way through the trachea, oesophagus and the stomach into the intestine, following the same course as the hookworm larva. Several times I have examined very carefully the abdominal and pleural cavities of rats soon after infection through the skin, washing with normal saline, without ever finding any of the larvae.

## IV. PARASITIC STAGES.

### 1. Outline of Parasitic Development.

#### (*a*) *General Considerations.*

The larvae of *H. muris* after penetration into the host develop very rapidly. They reach sexual maturity in five to six days after infection and eggs are found in faeces after six to seven days.

From the morphological and biological view point, the parasitic life of this species can be divided into three stages, viz., the third larval stage, or the first parasitic stage; the fourth larval stage, or the second parasitic stage; and the stage of the adult worm, or the third parasitic stage. These stages are separated by two moults. On account of the great complication of the parasitic development I will first give a general outline of the changes which go on, and will then describe in detail the development of certain of the organs.

### (*b*) *The First Parasitic Stage or the Third Larval Stage.*

The first parasitic stage of *H. muris* begins at the moment of penetration of the mature larvae into the host and is divided from the second parasitic stage (fourth larval stage) by the second ecdysis. This stage is not separated from the second larval stage by a moult but is differentiated from it by a complete change of environment which initiates profound morphological changes. The larvae after penetrating into the host are found first in the lungs of the host in about 14 to 20 hours. Usually they remain for about 35 to 50 hours in the lungs since they are found in this location until 50 to 65 hours after infection. Exceptionally, larvae were found in the lungs of the host 72 hours after infection. Toward the end of their sojourn in the lungs the second moult begins.

The structural changes which take place during the first parasitic stage may be summarized as follows (Fig. 7, Plate VIII and Text-fig. 3 *a* and *b*):

(1) The larvae grow rapidly, increasing more in width than in length.

(2) The buccal-cavity becomes shorter and wider.

(3) The oesophagus increases in length.

(4) The cells of the intestinal wall increase in thickness and in number. They come to contain so much pigment that their nuclei cannot always be detected.

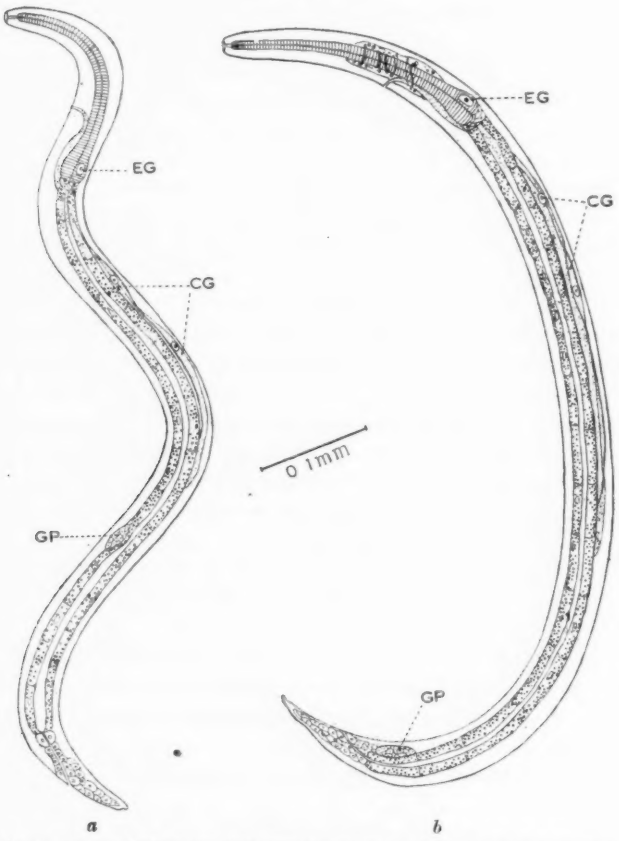
(5) The excretory system becomes clearly differentiated. The cervical glands are now seen dorsally in the body-cavity at the anterior region of the intestine, and the excretory pore can be distinguished on the ventral surface in the oesophageal region.

(6) The differentiation of the sexes occurs during this stage.

### (*c*) *The Second Moult.*

The second moult occurs usually toward the end of the life in the lungs. The preparation for this moult begins from 35 to 40 hours after infection, and the process of moulting extends over a period of from 12 to 15 hours. The larvae at the time of moulting move very slowly and become somewhat coiled. In observing some larvae in the process of moulting, I noticed that a longitudinal rupture of the old cuticula occurred at the base of the oesophagus. Through this opening the larva gradually worked its way sideways, withdrawing the anterior end from the anterior region of the cuticula and in so doing invaginating the cuticula of this region like the finger of a glove. It is not

uncommon to see a larva carrying around the old skin out of which it has partly wriggled. When they cast the old cuticula they become very active and soon after start their migration toward the intestine of the host. The larvae which are found in the lungs are always in the first parasitic stage or in the moult, while in the intestine some will be found in the second parasitic stage.




Text-fig. 3. Larvae during the first parasitic stage in the lungs of an experiment rat, 35 hours after infection. *a*, Male; *b*, female.

The structural changes which occur during the moulting process are as follows:

(1) The buccal-cavity loses its cylindrical shape and becomes greatly reduced in size.

(2) The oesophagus extends almost up to the anterior end of the body.

(3) The characteristic cuticular expansion arises at the anterior end of the body.

### (*d*) *The Second Parasitic Stage or the Fourth Larval Stage.*

The larvae in the second parasitic stage (fourth larval stage) always reach the intestine of the experimental rats soon after the casting of the old cuticula. Usually they travel from the lungs to the intestine about 50 to 60 hours after infection. Sometimes they are found in the intestine as early as 45 hours after infection, while in some cases they remain in the lungs undergoing moulting as long as 72 hours after infection. The growth of the larvae during this stage is very rapid, and they soon start the third ecdysis and reach the adult stage. It is during this stage that the sexual organs develop with remarkable rapidity as will be described in a later section.

### (*e*) *The Third Moult.*

The third moult usually begins from 90 to 108 hours after infection and lasts for about 12 to 15 hours. The larvae in the moult are found somewhat coiled. The structural changes which occur during the third moult are as follows:

(1) The newly formed cuticula is provided with prominent longitudinal markings in the form of ten ridges.

(2) The reproductive organs become fully formed.

### (*f*) *The Third Parasitic or Adult Stage.*

Shortly after completion of the third ecdysis, the larvae reach sexual maturity. The mechanism of the casting of the cuticula does not differ from that of the previous moult. The ecdysis of the female occurs a little later than that of the male. The structure of the adult worm will not be included in this paper, because it has been described in my previous paper (Yokogawa, 1920). During this stage there are two layers of the cuticula, the outer apparently representing the fourth moult, but never being shed.

## 2. SPECIAL DESCRIPTION OF THE DEVELOPMENTAL CHANGES DURING THE PARASITIC STAGES.

### (*a*) *Size, Shape and Colour.*

*Size.* The larva, after penetration into the host, increases very rapidly in size. At the beginning of the first parasitic stage the increase in width is especially marked while the increase in length is greatest during the later stages. After the sexes are differentiated the female is almost always larger than the male. The moults of the females in the parasitic stages come a little later than those of the males. Table IV indicates the size of both sexes at the beginning of the parasitic stages.

Table IV.

*The Size of the Males and Females of* H. muris *at the beginning of the Parasitic Stages.*

| Stages | Age of the larvae (duration after infection) | Sex | Length (mm.) | Width (mm.) |
|---|---|---|---|---|
| First parasitic stage | 15 hours | Sexes cannot yet be distinguished | 0·68 | 0·032 |
| | | | 0·68 | 0·032 |
| | | | 0·70 | 0·028 |
| | | | 0·71 | 0·029 |
| | Average size | | 0·69 | 0·030 |
| Second parasitic stage | 58 hours | ♂ | 1·43 | 0·054 |
| | 60 ,, | ♂ | 1·75 | 0·061 |
| | ,, ,, | ♂ | 1·29 | 0·052 |
| | ,, ,, | ♂ | 1·28 | 0·052 |
| | Average size | ♂ | 1·437 | 0·0547 |
| | 60 hours | ♀ | 1·93 | 0·056 |
| | 63 ,, | ♀ | 1·45 | 0·052 |
| | ,, ,, | ♀ | 2·08 | 0·065 |
| | ,, ,, | ♀ | 2·65 | 0·060 |
| | Average size | ♀ | 2·027 | 0·0582 |
| Third parasitic stage | 120 hours | ♂ | 4·70 | 0·100 |
| | ,, ,, | ♂ | 4·52 | 0·130 |
| | ,, ,, | ♂ | 3·425 | 0·100 |
| | 140 ,, | ♂ | 3·625 | 0·115 |
| | Average size | ♂ | 4·067 | 0·111 |
| | 120 hours | ♀ | 4·85 | 0·095 |
| | ,, ,, | ♀ | 5·60 | 0·125 |
| | 140 ,, | ♀ | 6·30 | 0·125 |
| | ,, ,, | ♀ | 4·63 | 0·090 |
| | Average size | ♀ | 5·344 | 0·109 |

As shown in Table IV the female is more slender in proportion to the length than the male.

*Shape.* The changes in shape which take place during the parasitic life occur in the following order. At the beginning of the first parasitic stage, the shape does not differ to any extent from that of the mature larvae in the free life. They soon increase, however, much more in width than in length, so that the shape appears quite different from that of the mature free-living larva (cf. Figs. 6 and 7, Plate VIII). During the second parasitic stage the larvae grow rapidly and many characteristic changes in shape can be noted. The anterior end is small and the cuticular expansion, which is a differentiating character of the genus Heligmosomum, makes its appearance. The length of this cuticular expansion in the second parasitic stage is 0·025 mm. to 0·037 mm., while in the next stage (adult) it measures 0·06 mm. to 0·07 mm. in length.

The shape of the posterior ends of the larvae early in the second stage begins to show the sexual differentiation which becomes so prominent later.

*Colour.* The cuticula of the larvae in the first parasitic stage is colourless while that of the adult worm is pinkish. The cuticula of the larvae in the second parasitic stage has a slightly yellowish tinge. They appear, however, at this stage as black or dark-brown spots or as curved strings on the mucous membrane of the intestine of the host, since the dense pigment of the intestinal cells shows through and gives its colour to the whole worm when examined with the naked eye. After completion of the third ecdysis, the colour of the cuticula not only increases in intensity but takes on the pinkish shade. As noted above the cuticula consists at this stage of two separate layers. These layers, the outer one of which probably represents an incomplete moult, have the same colour. The outer cuticula is much wider than the inner. The cuticula appears to have a yellowish-red colour when seen with transmitted light under the microscope, while it has a reddish or pinkish appearance by reflected light.

### (*b*) *The Cuticula.*

The cuticula of the larva in the first parasitic stage does not differ from that of the mature free-living larva. It consists of a thin transparent membrane with closely set striations. When the larvae reach the next stage, the anterior part of the cuticle inflates and makes a peculiar cephalic area, the cuticular expansion. This cuticular expansion or the cephalic area consists of very thin cuticula without any striations. The other regions of the cuticula are relatively thick and have the transverse striations except the posterior inflation of the male which later forms the bursa. In this inflated bursal region the cuticula becomes thinner and thinner as the expansion increases.

After the completion of the third ecdysis, the cuticula shows prominent longitudinal markings in the form of ten ridges. These longitudinal ridges begin a little behind the cephalic area and run parallel to the posterior end. At this stage, the transverse striations are not continuous around the cuticula but are found only on the longitudinal ridges. During this stage, the cuticula becomes looser and looser and a new cuticula similar to that produced in moulting develops under the old. The old cuticula finally separates from the new and a relatively wide space develops between them. Especially at the posterior end of the female, the outer cuticula is widely separated from the inner and forms a peculiar sac surrounding the anus and the vulva.

The inner newly-formed cuticula has only transverse striations and not the longitudinal ridges which are so prominent on the outer cuticula. These two layers of cuticula are fused at the anterior tip, at the posterior limit of the cephalic inflation, at the anus and vulva of the female and over the whole of the bursa of the male. At all other parts of the body they are widely separated.

(*c*) *Digestive System.*

*The mouth and buccal-cavity.* The buccal-cavity of the larva in the first parasitic stage becomes shorter and wider than that of the mature, free-living larva. The anterior end of the larva at this stage becomes wider and blunter and the prominent edge of the mouth, which was recognizable in the earlier stage, disappears. With the increase in size of the anterior end the mouth expands more rapidly than the buccal-cavity, making this cavity funnel-shaped. The length of the buccal cavity of the larvae in the first parasitic stage is 0·005 mm. to 0·008 mm., while in the mature free-living larvae it had a length of 0·009 mm. to 0·019 mm.

After the completion of the second ecdysis, the buccal-cavity is almost obliterated by the forward growth of the oesophagus, only a very small space being left.

After the disappearance of the larval buccal-cavity, the mouth cavity of the adult stage is found at the anterior end of the body, surrounded by the inflated cuticula and the subcuticular layer (Text-fig. 1 *b*).

*Oesophagus.* The oesophagus of the larvae in the parasitic life is conoidiform and its length can be modified in an individual worm by contraction of the body. At the beginning of the first parasitic stage it measures about 0·17 mm. to 0·19 mm. in length, while it is about 0·27 mm. to 0·32 mm. long at the beginning of the next stage. After the completion of the third ecdysis, the oesophagus measures from 0·35 mm. to 0·45 mm. in length.

*Oesophageal glands.* After infection, the granular strands which represent the substance of the oesophageal glands increase in number as described by Looss (1905, pp. 88 and 89) for the hookworm, and the subventral gland-cells become hard to see, being covered with the granules, while there can be seen a large vesicular ovoid nucleus at the dorsal side of the posterior end of the oesophagus (Fig. 7, *eg*, Plate VIII).

*Intestine.* There are remarkable changes in structure of the intestine of the larvae soon after the beginning of parasitic life. The cells of the intestinal wall become greatly thickened, become loaded with pigmented granules, and also increase in number (Fig. 7, Plate VIII and Text-fig. 3 *a* and *b*). I found in one specimen from the lungs of an experimental rat 15 hours after infection that one side of the intestine consisted of twelve cells, while the other side was composed of fourteen cells. It is evident that the cells divide as development proceeds since a greater number of cells are found in the intestinal wall of the larvae in more advanced stages. The intestinal cells of the larvae in the parasitic life are so dark and crowded with granules that it is difficult to see the nuclei. At the anterior limit of the intestine there are found in the parasitic stages the small clear cells which are the cells of the intestinal valve, which were present in this region in the free-living larvae.

*Rectum.* The morphological changes in the rectum of the larvae during the parasitic stages of development are very great and differ in the two sexes,

since they are influenced by the development of the external sexual organs. In the male 15 hours after infection the rectum runs obliquely to the main axis of the body through a definite cell group. Later a space develops between the walls of the rectum and this cell group. This space (Fig. 9, *rs*, Plate IX) is clearly defined in specimens found 30 hours after infection, while it has not yet appeared in specimens within 24 hours after infection. The wall of the rectum consists of a thin membrane. The rectum of the larvae near the beginning of the first parasitic stage has a length of about 0·04 mm. while its length has increased to between 0·18 to 0·20 mm. by the end of the second parasitic stage. The space surrounding the rectum and also the rectal lumen becomes wider as the bursa develops. Toward the end of the second parasitic stage a cell situated dorsally to the rectal sphincter grows posteriorly along the dorsal side of the rectum (Fig. 15, *pwc*, Plate IX). At the same time a cell on the ventral side of the end of the ejaculatory duct extends posteriorly a short distance along the inside of the ventral wall of the body (Fig. 19, Plate X). These cells become thicker and from them is produced the wall of the cloaca of the adult male. With the completion of the third ecdysis, the membranous wall of the rectum breaks off from the thicker part and forms a peculiar cloaca.

The structural changes of the rectum during the development of the female in the parasitic life are not as complicated as those of the male. In the beginning of the parasitic life, the tail of the female is usually curved ventrally. The rectum runs obliquely through a cell group to the anus, and has a length of about 0·04 mm. (Fig. 22, Plate XI). The cell group surrounding the rectum grows until about the middle of the second parasitic stage and then gradually the cells seem to decrease in size and the number diminishes. At the beginning of the second parasitic stage, a cell which is situated just back of the anus projects very slightly (Figs. 27 and 30, *pac*, Plate XI). This projection is gradually seen to disappear as the cells of the tail degenerate. After the completion of the third ecdysis the cells of the tail region lose their definite differentiation and nuclei are no longer visible (Fig. 31, Plate XI). The rectal lumen at this stage is lined with a definite chitinous membrane, and the rectum has a length of 0·02 to 0·03 mm. The tail of the adult female is very thin, curves ventrally like a hook and is surrounded by the peculiar sac formed from the loose folds of the outer cuticula.

### (*d*) *The Excretory System.*

The excretory apparatus of *H. muris* was not worked out in detail but seemed to be similar to that system as described for other species of the family Strongylidae. I gained, however, some information on the development of this system during the course of my studies which will be included here. Only the excretory pore, the cervical glands, and the excretory vesicle were found. The excretory pore is situated on the ventral surface at a distance of 0·15 to 0·25 mm. from the anterior end of the body, according to the stage of development. The excretory vesicle can be seen in the anterior region of the

body extending a little in front of the excretory pore and connected with it by a short duct. The cervical glands could be very clearly distinguished in the living larvae of the parasitic stages, although they were difficult to see in the sexually mature worms. In the specimens from the experimental rats 15 to 20 hours after infection, the protoplasm of the cervical gland cells is not granular while in later stages it contains many granules. These gland cells (Fig. 7, Plate VIII and Text-fig. 3 *a* and *b*) are located in the dorsal body-cavity and extend along the dorso-lateral sides of the chyle intestine. The anterior ends of the cervical glands are narrower than their posterior ends, and they seem to be connected with the "bridge" as Looss (1905, pp. 104 and 105, Fig. 30) shows in *Ancylostoma duodenale* at the ventra-lateral side of the oesophagus.

These cells have an elongate lancet shape, and extend to about the middle of the body. They contain large transparent ovoidal nuclei, which lie in the centre of the glands. Each nucleus has a round nucleolus. As the reproductive organs extend forward in development the cervical gland cells become more difficult to see since they are crowded to the side by the anterior part of the ovary or the testis as the case may be.

### 3. Sexual Differentiation and the Development of the Reproductive Organs.

#### (*a*) *General Discussion.*

The post-embryonic development of the reproductive organs of nematodes is very insufficiently known. *H. muris* offers very good material for the study of these organs since they are simple in this species and the period of development is short. Therefore an especially careful study was made of the reproductive organs and a very large series of stages was examined.

The stage of development of the reproductive system does not always depend on the time elapsed after infection, but rather is correlated with the degree of growth in size. There are of course some variations in the development of this system in animals of about the same size. I will describe the average condition which has been ascertained from a very large series of specimens.

Looking in the literature on the development of the nematodes, nothing is known particularly regarding the development of the internal and the external sex-organs, while in the higher animals they develop from two different origins, one part from the genital anlage, while the other without reference to the genital primordium. Neuhaus (1903) who investigated the post-embryonal development of the *Rhabditis nigrovenosa* described that the vagina might be developed from the middle part of the genital primordium, while Leuckart (1887) described that the vagina of *Allantonema* is formed by a projection of the ventral wall. The argument of Neuhaus is based on the position of the vagina in the body and the identity of the cells.

Looss (1897 and 1911) did not add to the knowledge of this point in the development of nematodes even though he studied on the development of *Ancylostoma*, *Strongyloides* and *Rhabdonema*. Veglia (1915) who studied the life-history of the *Haemonchus contortus* added but little to the knowledge of the development of the reproductive organs. Theiler and Robertson (1915), who worked on the life-history of the wire-worm in Ostriches, mentioned briefly the development of its bursa and vulva. They described the development of the vulva as follows: "The central cell is the biggest of the lot of the female primordium; ventrally it soon splits crossways to the longitudinal axis, indicating the future vulva. This cell is also raised slightly above the adjoining ones and reaches the subcuticula. In a somewhat more advanced stage this slit is surrounded by a number of cells." Their description is inadequate and their explanation of the development of the vulva seems unreasonable. They described also very briefly the formation of the bursa. As far as it goes their descriptions agree with what has been found in *H. muris*. I studied very carefully and made clear the development of the reproductive apparatus, and knew that the testes, vas deferens, seminal vesicle, cement gland and the ejaculatory duct develop from the male primordium, while the bursa, spicules and the gubernacles are produced without reference to the genital primordium. Accordingly I shall call the former the internal sex-organs, and the latter the external sex-organs. I also found that the ovary, oviduct, seminal receptacle, uterus and ovijector (houstrix) are produced from the genital primordium, while the vulva and the vagina develop from outside the genital primordium. The second part of the ovijector is produced from the distal end of the genital primordium and the anterior part of the vagina, that is, this part corresponds to the adjoining part of the internal and external sex-organs.

(*b*) *The Beginning of Sexual Dimorphism.*

Sexual dimorphism has not been noted for the free-living larval stages of the Strongylidae. Looss (1911) criticized the suggestion of several authors who tried to distinguish the sexes in free-living nematode larvae by the shapes of their tails. He concluded that sexual dimorphism cannot be detected in the free-living larvae of the nematodes. Looss (1911) on the *Ancylostoma*, Theiler and Robertson (1915) on the wire-worm in Ostriches, and Veglia (1915) on the *Haemonchus contortus*, do not describe the beginning of sexual dimorphism, and so far as I know there is no literature on this subject. I think it is very interesting and important matter to learn just when and how the sexual differences appear during the parasitic life. Sexual dimorphism in *H. muris* was distinguished in very young larvae during the first parasitic stage (Text-fig. 3 *a* and *b*).

Three essential points of difference between the sexes were determined at this early stage, i.e., first, the posterior migration of the genital primordium of the female; second, structural differences in caudal regions; and third, differences in the shape of the genital primordia.

In the first larval stage, the genital primordium is located at about the middle of the body. After the completion of the first moult, its position is a little behind the middle part of the body on account of the relative reduction in the length of the posterior part of the body, and the considerable increase in the length of the oesophagus (see Table II).

Table V shows the backward shifting of the position of the genital primordium during free life.

Table V.

*The Position of Genital Primordium during Free Life.*

| Stages in free life | Body (length) (mm.) | Body (width) (mm.) | Size of germ cell group (mm.) | Position of germ cell group (dist. from ant. end) | Percent. of distance from anterior end |
|---|---|---|---|---|---|
| First larval stage | 0·280 | 0·015 | 0·006 × 0·004 | 0·148 | 52·8 |
| | 0·300 | 0·018 | 0·006 × 0·004 | 0·153 | 51·2 |
| | 0·395 | 0·018 | 0·007 × 0·004 | 0·202 | 51·3 |
| | 0·442 | 0·022 | 0·007 × 0·004 | 0·235 | 53·2 |
| First moult | 0·660 | 0·034 | 0·010 × 0·005 | 0·330 | 50·0 |
| | 0·680 | 0·032 | 0·008 × 0·005 | 0·340 | 50·0 |
| | 0·700 | 0·033 | 0·010 × 0·006 | 0·376 | 53·0 |
| | 0·720 | 0·034 | 0·010 × 0·005 | 0·387 | 53·7 |
| | 0·750 | 0·034 | 0·012 × 0·006 | 0·387 | 51·6 |
| Second larval stage (the mature free-living larvae) | 0·680 | 0·028 | 0·016 × 0·008 | 0·390 | 57·3 |
| | 0·715 | 0·026 | 0·016 × 0·007 | 0·420 | 58·7 |
| | 0·740 | 0·026 | 0·017 × 0·008 | 0·435 | 58·7 |
| | 0·630 | 0·025 | 0·012 × 0·008 | 0·382 | 60·6 |
| | 0·715 | 0·025 | 0·014 × 0·008 | 0·420 | 58·7 |

As shown in Table V the genital primordium of the mature free-living larvae is situated near the middle body and no differences in its position can be noted between the sexes. After infection a remarkable differentiation of position of the genital primordium in the sexes comes about. Examining many specimens in parasitic stages, I found that the genital primordium of the female migrates from near the middle of the body toward its posterior end, while that of the male does not migrate but remains near the middle of the body. This remarkable migration of the genital primordium of the female takes place between 20 to 30 hours after infection. By 30 hours after infection the genital primordium of the female has reached a position just in front of the anus (Text-fig. 3 *b*). Table IV shows the progress in this migration comparing the position of the genital primordium in both sexes at various times after infection.

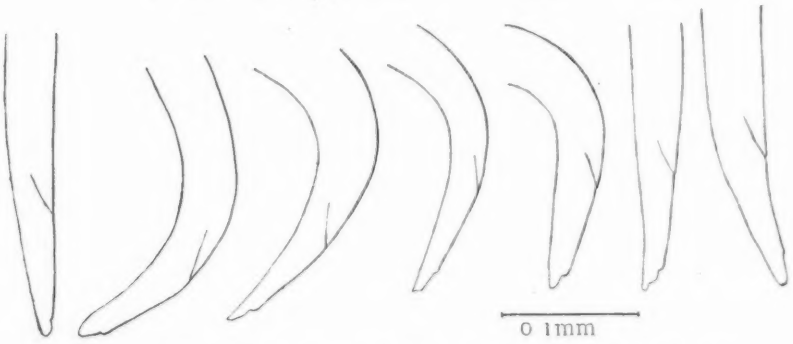
From Table VI it can be seen that as early as from 24 to 30 hours after infection the males and females are differentiated by the position of the genital primordium.

Finding many varying shapes of the tail of the mature free-living larvae (Text-fig. 4) I tried in vain to establish a sexual dimorphism in this character. I finally came to the conclusion that these differences were nothing but individual variation. I found, however, structural differences between the posterior ends of the sexes very early in the parasitic development. The posterior end

Table VI.

*Position of Genital Primordium from 15 to 30 hours after Infection.*

| Age of larvae | Body (length) (mm.) | Body (width) (mm.) | Size of genital primordium | Position of gen. primordium (distance from anterior end) | Percent. of distance from ant. end | Sex |
|---|---|---|---|---|---|---|
| 15 hours after infection | 0·680 | 0·032 | 0·016 × 0·009 | 0·390 | 57·3 | ? |
| | 0·680 | 0·032 | 0·014 × 0·006 | 0·391 | 57·5 | ? |
| | 0·702 | 0·028 | 0·018 × 0·01 | 0·410 | 58·4 | ? |
| | 0·710 | 0·029 | 0·015 × 0·008 | 0·405 | 56·3 | ? |
| 24 hours after infection | 0·885 | 0·032 | 0·016 × 0·007 | 0·550 | 62·1 | ? |
| | 1·030 | 0·033 | 0·018 × 0·007 | 0·600 | 58·3 | ♂ |
| | 0·820 | 0·030 | 0·021 × 0·010 | 0·510 | 62·2 | ? |
| | 0·780 | 0·028 | 0·021 × 0·010 | 0·450 | 57·7 | ♂ |
| | 0·825 | 0·031 | 0·021 × 0·010 | 0·485 | 58·7 | ? |
| | 0·755 | 0·030 | 0·017 × 0·006 | 0·490 | 65·0 | ? |
| | 0·970 | 0·032 | 0·024 × 0·01 | 0·750 | 77·3 | ♀ |
| | 0·985 | 0·031 | 0·028 × 0·007 | 0·865 | 88·0 | ♀ |
| | 0·790 | 0·032 | 0·028 × 0·008 | 0·565 | 71·5 | ♀ |
| | 1·09 | 0·035 | 0·031 × 0·01 | 0·940 | 86·2 | ♀ |
| 30 hours after infection | 0·825 | 0·032 | 0·017 × 0·008 | 0·421 | 51·6 | ♂ |
| | 0·800 | 0·030 | 0·025 × 0·01 | 0·432 | 54·0 | ♂ |
| | 0·825 | 0·031 | 0·017 × 0·011 | 0·463 | 56·7 | ♂ |
| | 0·800 | 0·036 | 0·024 × 0·01 | 0·437 | 54·6 | ♂ |
| | 0·950 | 0·035 | 0·028 × 0·01 | 0·544 | 57·2 | ♂ |
| | 0·988 | 0·032 | 0·03 × 0·011 | 0·500 | 50·6 | ♂ |
| | 0·975 | 0·036 | 0·037 × 0·008 | 0·876 | 89·9 | ♀ |
| | 0·850 | 0·031 | 0·028 × 0·008 | 0·716 | 84·2 | ♀ |
| | 0·800 | 0·032 | 0·027 × 0·008 | 0·684 | 85·5 | ♀ |
| | 0·900 | 0·030 | 0·024 × 0·006 | 0·783 | 87·0 | ♀ |




Text-fig. 4. Posterior ends of free-living mature larvae showing the various shapes.

of the male becomes more curved than that of the female, and the arrangement of the cells in this region is different. Comparing many specimens found in the lungs of the experimental rats from 15 to 23 hours after infection, I found the following differences in the caudal regions of the sexes (cf. Figs. 8 and 22, Plates IX and XI).

1. The rectum in the male is surrounded by 10 cells excepting the cells of the rectal ligament and sphincter, while that of the female is surrounded by only five cells excepting the same cells.

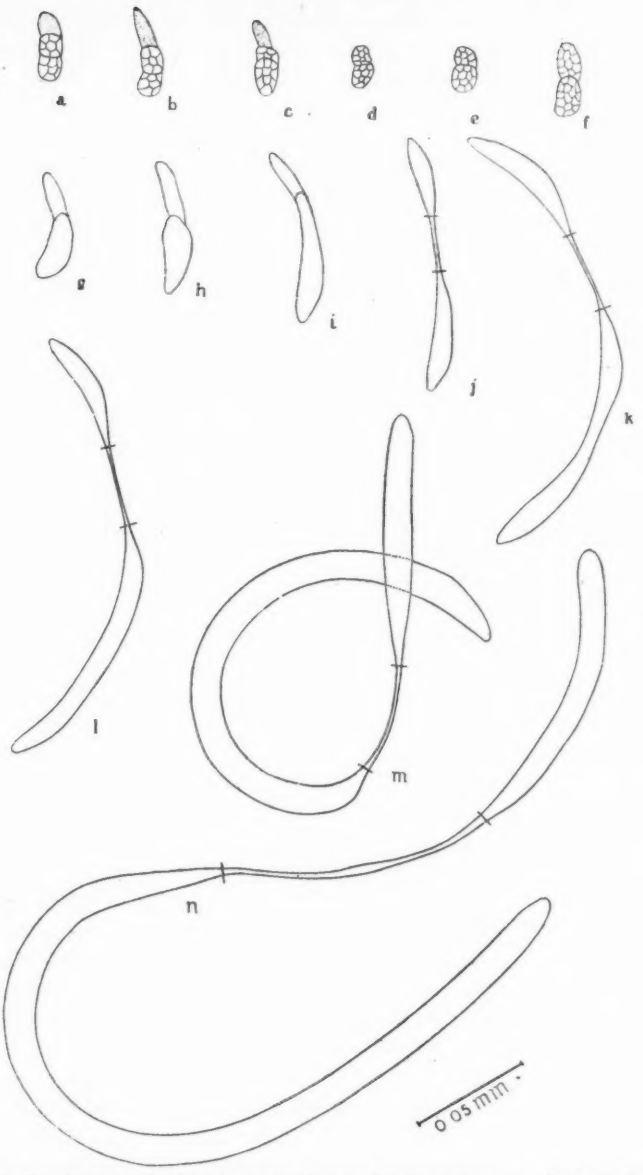
2. The subcuticular layer of the ventral wall just in front of the anus of the male does not at this time show any cell-divisions, while in this region of the female already three or more cells can be distinguished.

In the youngest free-living stages the genital primordium apparently consists of two cells. It is a small ovoid body, measuring about 0·006 mm. by 0·004 mm. It develops gradually with the development of the body. In the mature free-living larvae the genital primordium consists of six to eight cells and has a size of 0·012 mm. to 0·017 mm. by 0·006 mm. to 0·008 mm. In this stage its shape varies and it almost always has at its anterior end a small more or less dark body as is shown in the figure (Text-fig. 2). In a few cases this unknown body was found at the posterior end of the genital primordium. After infection, the genital primordium becomes gradually transformed in size and in general appearance according to the stage of development and early shows sexual differences. In the female it appears spindle-shaped in the first parasitic stage, while in the male it is rather oblong in shape (Text-figs. 5 and 7). This difference is clearly defined 24 hours after infection. At this time the small darker body described above is found usually at the anterior part of the genital primordium of the male, while it rarely can be seen in the female.

### (c) *The Development of the Male Reproductive Organs.*

### (1) The Internal Sex-Organs.

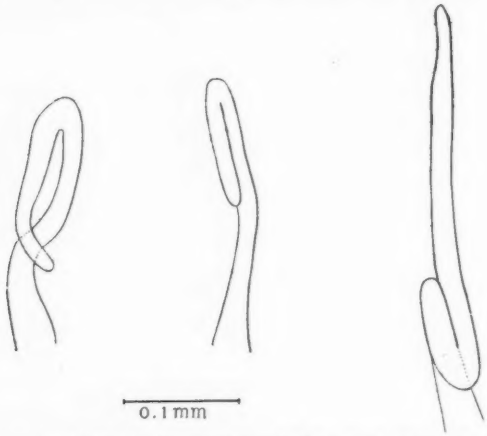
*General description.* The term "internal sex-organs" is used to refer to the organs which develop from the genital primordium, that is, the testis, vas deferens, seminal vesicle, cement gland and ejaculatory duct. As stated in the previous section, the genital primordium of the male is situated ventrally near the middle of the body. Toward the end of the first parasitic stage it becomes separated into two parts by an extremely delicate strand of tissue. The beginning of this division can be distinguished early by a slight constriction in the middle of the genital primordium (Text-fig. 5). The division of the genital primordium usually occurs in 40 to 50 hours after infection and sometimes later. After division the posterior part develops more rapidly than the anterior one growing toward the posterior end of the body. When the young male enters the second parasitic stage the end of this posterior division of the reproductive primordium has grown back to the end of the chyle intestine. After growing to this point the anterior end of the posterior part of the genital primordium grows forward. Meanwhile, the anterior part grows anteriorly along the ventral side of the intestine. Toward the end of the second parasitic stage, and especially during the last moult, the anterior part of the reproductive body develops very rapidly, crossing the middle part of the intestine and growing forward. By the completion of the last ecdysis it reaches almost to the anterior end of the chyle intestine.




Text-fig. 5. Development of primordium of male reproductive system. *a–c*, First parasitic stage, 24 hours after infection; *d* and *e*, first parasitic stage, 30 hours after infection, length 0·825 mm.; *f*, first parasitic stage, 45 hours after infection, length 0·65 mm.; *g*, first parasitic stage, 35 hours after infection, length 1·13 mm.; *h*, first parasitic stage, 50 hours after infection, length 1·08 mm.; *j*, second stage, 40 hours after infection, length 1·1 mm.; *k*, second parasitic stage, 45 hours after infection, length 1 mm.; *l*, second parasitic stage, 54 hours after infection, length 1·11 mm.; *m*, second parasitic stage, 52 hours after infection, length 1·45 mm.; *n*, second parasitic stage, 60 hours after infection, length 1·75 mm.

In the beginning of the second parasitic stage, the internal reproductive system of the male shows little, if any, differentiation, and appears as a tube of clear cells, separated into two parts by a narrow strand of tissue. In the course of the second parasitic stage (Fig. 18, *agp* and *pgp*, Plate X) the cells of its posterior part become larger and clearer than those of the anterior one, and become arranged in two rows, while the cells of the anterior part remain small and are arranged irregularly. Then the narrow part becomes gradually shorter and broader. Finally all parts of the internal sex-organs become clearly differentiated.

*Development of the testes.* It is interesting to note that the testis in *H. muris* develops from only the anterior half of the male genital primordium and the other internal organs from its posterior half. As mentioned above, the anterior part of the genital primordium is separated from the posterior part by an




Text-fig. 6. Variations in the anterior end of the testis of the adult male.

extremely delicate strand of tissue, and at the beginning of the first parasitic stage the cells of this part are not yet differentiated (Fig. 17, Plate IX). During the second parasitic stage the cells of the anterior part of the genital primordium gradually become smaller and more numerous, while those of its posterior part increase in size. Toward the end of the second parasitic stage and especially during the last moult the anterior part which forms the testis develops very rapidly, crossing the chyle intestine at the middle of the body and extending anteriorly along the dorsal side of the intestine. After the completion of the third ecdysis, the testis is fully developed and spermatozoa can be distinguished at its proximal end. Its anterior end reaches nearly to the base of the oesophagus, forming a loop of various shapes (Text-fig. 6). The free anterior end of the testis is usually more blunt and broader than that of the ovary.

*Development of the vas deferens.* The vas deferens develops from the narrow region which is situated between the anterior and the posterior parts of the

genital primordium (Fig. 17). At the beginning of the first parasitic stage it is represented only as an extremely fine strand of tissue. Then this tissue strand becomes a little larger, taking the shape of a small tube with one spindle-shaped cell in each side (Fig. 17). The length of this narrow central region varies greatly in different specimens. This region at the beginning of the division of the genital primordium is short, having a length of 0·02 to 0·04 mm. At the beginning of the second parasitic stage it has become much extended, measuring 0·06 to 0·0115 mm. in length, and then it shortens again, showing a tubular structure. Toward the end of the second parasitic stage it becomes much broader, with two cuboid cells on each side of its wall, where previously there was only one spindle-shaped cell (Fig. 20, *vd*, Plate X). These cuboidal cells are close together and are separated from the adjoining cells both anteriorly and posteriorly by definite constrictions (Fig. 20, *vd*). These constrictions become less clearly defined with later development. The fully developed vas deferens is narrower than the other regions of the male reproductive organs, having a length of about 0·02 to 0·03 mm. and is situated on the dorsal side of the intestine near the middle of the body.

*Development of the seminal vesicle.* The seminal vesicle develops from the anterior region of the posterior part of the genital primordium. At the beginning of the second parasitic stage it is not clearly differentiated. Toward the end of the second parasitic stage and especially during the last moult the region just behind the vas deferens has a wall consisting of clear cuboidal cells, while the part just beyond is lined with high columnar cells containing fine granules. The seminal vesicle (Fig. 20, *sv*) is produced from the region lined with the clear cuboidal cells and becomes a large tube with a wide lumen. The cells of the wall of this region decrease in thickness with the increasing of the lumen, and finally a thin membrane is produced in which it is difficult to make out the individual cells. At this time the lumen of the seminal vesicle contains a few sperms. The seminal vesicle of the adult worm is situated at the dorsal side of the intestine near the middle part of the body, and has a length of about 0·1 to 0·13 mm., and is filled with spermatozoa.

*The development of the cement gland.* With the formation of the seminal vesicle the region which is to form the cement gland becomes more clearly defined. This region is lined with high columnar cells which at first are all alike. Each of these cells contains a round nucleus and many fine granules. When the internal sex-organs are almost developed the cement gland becomes differentiated into two parts by the appearance of the cells of its wall (Fig. 20, *cmg*, Plate X). The cells of its posterior half become darker than those of its anterior half and contain a great amount of granules. In the adult worm, this gland usually is situated where the reproductive tube crosses the intestine, while in the earlier stages it is found farther back, on the ventral side of the intestine.

*The development of the ejaculatory duct.* The ejaculatory duct is produced from the posterior part of the genital primordium. The cells of its wall early

become cuboidal in shape and are transparent (Figs. 12 and 13, *ed*, Plate IX). This part is found always along the ventral side of the intestine and its posterior end projects into the cloaca at the ventral side of the rectum.

## (2) The External Sex-Organs.

*General discussion.* The term "external sex-organs" is used to refer to the organs connected with the reproductive processes in the male which do not develop from the genital primordium.

At the beginning of the parasitic life the number of cells in the tail and around the rectum of the male increases. As development proceeds these cells continue to increase in size and in number, and become re-arranged in a definite manner. It is from definite groups of these cells that the spicules, gubernacula and the rays of the bursa develop.

*The development of the bursa.* The cell group found in the posterior end of the male seems to have originated from the lateral bands and the muscle-cells, since they are located on the sides and show no relation to the ventral and the dorsal walls of the body as early as 24 hours after infection. With development these cells increase in size and number and a space is formed around the rectum (Fig. 9, *rs*, Plate IX). In the beginning of the first moulting the cells of the subcuticular layer at the ventral side of the tail region divide and join the other cells of this region, so that toward the end of the first parasitic stage the posterior end of the male filled up with clear cells with round nuclei (Fig. 10, Plate IX). During the moult following this stage these cells show a definite arrangement as shown in the figure (Fig. 11, Plate IX). Early the cell group which is situated just behind the rectum becomes separated and differentiated into elongate conical or spindle-shaped cells (Fig. 11, *cs*). The length of these cells increases as development proceeds and later they produce the spicules (Figs. 11–14, *cs*, and 15, *s*, Plate IX), while the other cells of this region later form the bursal rays.

After the completion of the second moult the space which has been formed around the rectum gradually expands from its posterior end, particularly toward the ventral and the lateral sides (Figs. 12–15 and 19, Plates IX and X). As this space expands the posterior end of the male becomes inflated into a sac lined with cells. Toward the end of the second parasitic stage the cells which line the posterior part of this bursal sac produce small finger-like projections which are the beginnings of the rays of the bursa (Fig. 16). At this time each ray consists only of the projection from a single cell. These projections already represent the number and have assumed the position of the fully developed rays. The bursa therefore consists only of the inflated posterior end of the male which is lined by cells and is separated from the true posterior end of the worm by a considerable space (Fig. 19). The rectum (Fig. 19, *r*) still opens at the posterior end of the bursal sac. During preparation for the third moult, the lobes of the bursa become separated into their final form and the closed bursal sac now consists only of the old cuticula. After the shedding of this skin the

bursal lobes are fully developed and entirely separated (Fig. 21, Plate X). The rays of both lateral lobes now consist of several cells and each ray has assumed its characteristic shape. The central dorsal ray usually consists of two cells, while the externo-dorsal rays are each made up of the projection from only one cell.

*The development of the spicules and the gubernacula.* The spicules and the gubernacula have the same origin. They are produced by the long conical or spindle-shaped cells situated just back of the base of the rectum (Figs. 11–15, *cs* and *s*, Plate IX). In the beginning of the second parasitic stage these cells increase in size, while toward the end of this stage they decrease in number and produce the chitinous material of the spicules and the gubernacula. The spicules are produced at the sides of these cells and become extended very rapidly forward along the dorsal side of the intestine. They later reach a muscle cell-group which is present dorsally at a distance from the posterior end of the body. These muscle cells develop into the retractor muscles of the spicules, and come from one original cell (Fig. 19, *rms*, Plate X). This original cell at the beginning of the second parasitic stage is spindle-shaped and is located at the dorsal side of the intestine at a distance of about 0·22 to 0·23 mm. from the posterior end of the body (Fig. 13, *rms*, Plate IX). It is connected with the cells at the base of the rectum and with the subcuticular layer by tiny fibres. This spindle cell divides as the development of the sex-organs proceeds, forming two groups of muscle cells (Fig. 19, *rms*). These are the retractor muscles and extend anteriorly along the dorsal wall of the intestine with the further development of the sex-organs. Toward the end of the second parasitic stage, they are found at a distance of about 0·53 to 0·56 mm. from the posterior end of the body and become attached to the spicules. The spicules when first produced are transparent and colourless, while in the adult stage they have a brownish golden colour. The anterior ends of the spicules are slightly thickened and are attached to the retractor muscles, while their posterior ends are united and project from the dorsal side into the cloaca, forming a small arc.

The gubernacula are produced from the chitinous substance in the distal portion of the spicules toward the end of the second parasitic stage.

### (*d*) *The Development of the Female Reproductive Organs.*

### (1) The Internal Sex-Organs.

*General description.* The term "internal sex-organs" of the female refers to those organs which develop from the genital primordium and includes the ovary, oviduct, seminal receptacle, uterus and the ovijector.

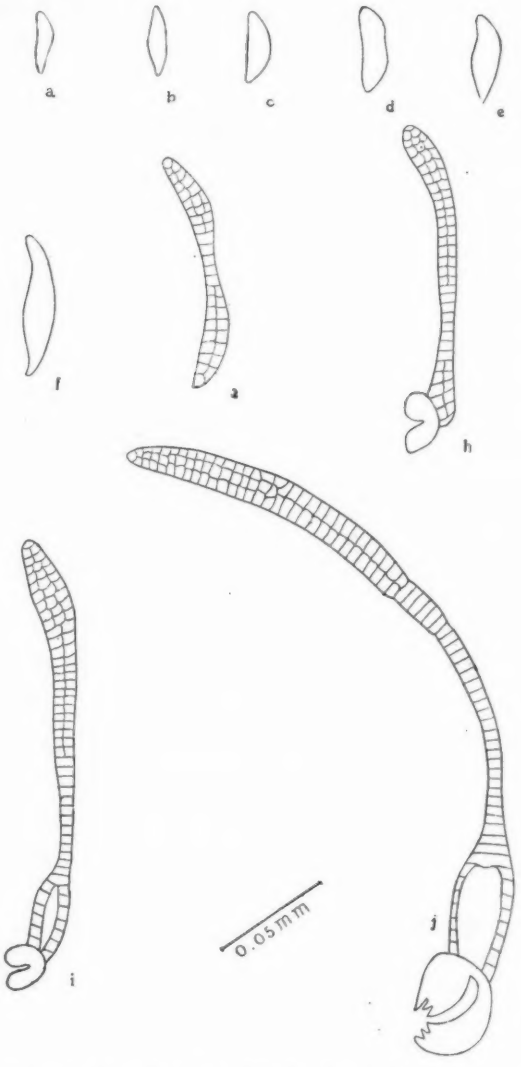
At the beginning of sexual differentiation, the genital primordium of the female migrates from the middle of the body to its posterior end. During this time, it can be found in different individuals in every position between the middle of the body and the anal region. After reaching a position just in front of the anus (Fig. 23, *gp*, Plate XI) the genital primordium increases in length,

growing forward (Fig. 24, *gp*, Plate XI). Toward the end of the first parasitic stage and especially during the second moult the female genital primordium increases considerably in length and begins to show differentiation (Text-fig. 7). At this time the subcuticular cells at the posterior portion of the body also increase in number. In the beginning of the second parasitic stage, the primordium of the ovary, seminal receptacle, uterus and the ovijector can be distinguished (Fig. 36, Plate XII). The oviduct is not differentiated from the posterior end of the ovary until the end of the second parasitic stage. During the first part of the second parasitic stage all of the internal sex-organs develop along the ventral side of the intestine, but toward the end of this stage the ovary increases very rapidly in length and crosses to the dorsal side of the intestine. As development proceeds most of the internal sex-organs grow over to the dorsal side of the intestine.

*The ovary.* The ovary develops from the anterior part of the genital primordium but there is no clear separation into two regions as in the development of the testes of the male. In the first part of the second parasitic stage the ovary grows forward slowly along the ventral side of the intestine (Fig. 36, *o*, Plate XII), while toward the end of this stage it crosses over and develops very rapidly along the dorsal side of the intestine. In the first half of the second parasitic stage (about 58 to 80 hours after infection) the size of the ovary increases from 0·08 to 0·9 mm. by 0·014 to 0·12–0·14 mm. by 0·014 to 0·015 mm., while during the last part of this stage and especially during the last moult (about 85 to 108 hours after infection) it develops from 0·14 by 0·014 mm. to 0·50–1·00 by 0·02 to 0·025 mm. In the beginning of the second parasitic stage the cells of the ovary are uniform in size. In the course of the second parasitic stage the cells in its posterior part increase in size and become arranged into two rows, while those of the anterior region are still small and closely packed (Fig. 36, *o*, Plate XII). During the last part of the second parasitic stage the ovary develops so rapidly that the wall of its posterior part comes to consist of flat cells, forming an empty tube. At this time the oviduct is formed from the posterior end of the ovary as will be explained in the following section. After the completion of the third ecdysis the ovary is fully developed.

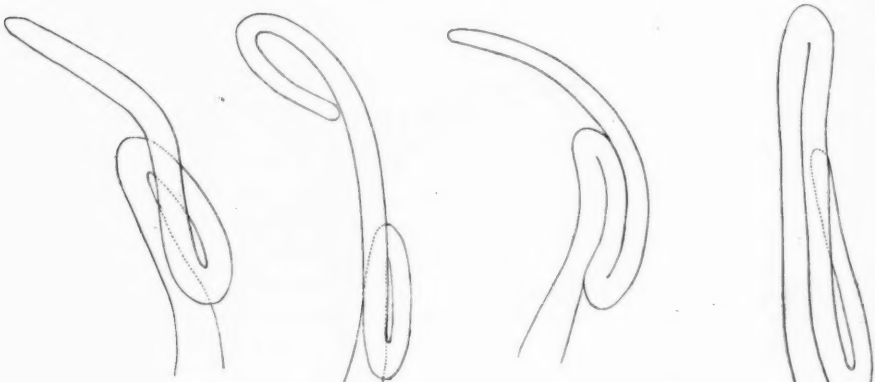
*The seminal receptacle.* The seminal receptacle develops from the region just behind the ovary. At the beginning of the second parasitic stage this part consists of a row of several cells which are a little larger than those of the uterus (Fig. 36, *sr*). At the end of the second parasitic stage the walls of the seminal receptacle consist of high columnar cells (Fig. 33, *sr*, Plate XII) having a size of about 0·10 by 0·025 mm., while the uterus and the posterior end of the ovary are lined by flat cells. By the time spermatozoa are introduced the seminal receptacle becomes a thin walled tube lined with flat cells. Its length in the adult worm is about 0·1 mm. and it joins the uterus without any sharp demarcation.

*The oviduct.* The oviduct is formed chiefly from the posterior end of the ovary. In the last part of the second parasitic stage the walls of the posterior




Text-fig. 7. Development of the primordium of the female reproductive system. *a*, First parasitic stage, 30 hours, 0·9 mm.; *b*, first parasitic stage, 40 hours, 0·98 mm.; *c*, first parasitic stage, 40 hours, 1·07 mm.; *d*, first parasitic stage, 40 hours, 1·02 mm.; *e*, first parasitic stage, 45 hours, 1·07 mm.; *f*, first parasitic stage, 35 hours, 1·21 mm.; *g*, second parasitic stage, 48 hours, 1·20 mm.; *h*, second parasitic stage, 52 hours, 1·4 mm.; *i*, second parasitic stage, 52 hours, 1·49 mm.; *j*, second parasitic stage, 72 hours, 1·89 mm.

end of the ovary consist of flat cells and this part becomes a vacant tube, while in the beginning it consisted of large cuboidal cells, showing a more or less large, rhombic space between the seminal receptacle and the ovary itself (Figs. 32 and 33, Plate XII). When the posterior portion of the ovary forms a vacant tube as described above, two pairs of spindle-shaped or triangular cells can be seen in its wall at a distance of about 0·04 to 0·06 mm. in front of the seminal receptacle (Fig. 36, *sr*, Plate XII). The region extending between these two pairs of cells and the seminal receptacle forms a muscular tube, the oviduct (Fig. 33, *ov*). Both ends of this tube are thickened, forming sphincters. The oviduct (Figs. 34 and 35, *ov*) seems to be an important factor in giving a definite form to the fully developed egg-cells as they pass along it singly on their way to the seminal receptacle. The length of the oviduct of the adult worm is about 0·07–0·09 mm.




Text-fig. 8. Variations in the anterior end of the ovary of adult female.

*The uterus.* The uterus develops from the cell-group which is situated between the primordium of the seminal receptacle and the ovijector. In the beginning of the second parasitic stage it appears as a row of several cuboidal cells which increases in length by the division of the cells of its anterior part (Figs. 26 and 27, *u*, Plate XI). The cells in the posterior portion of this row gradually increase in width and their centres become vacuolated (Figs. 28 and 36, *u*, Plates XI and XII); the increase in the size of these vacuoles produces the lumen of the uterus. Toward the end of the second parasitic stage the uterus is fully developed and forms a tube except at the posterior part which connects with the ovijector. After the completion of the third ecdysis fully developed egg-cells are found in the uterus, and in the posterior end of the uterus the wall is thickened to form a sphincter.

*The ovijector.* The ovijector (pars houstrix) develops from the posterior end of the genital primordium. Toward the end of the first parasitic stage, and especially during the second moult, it can be seen as a cell-group which consists of two to three pairs of cuboidal cells. After the completion of the second moult, that is, in the beginning of the second parasitic stage, it can be seen as a tube surrounded by two rows of 7 to 8 cuboid cells, which have a size of 0·027 to 0·041 by 0·015 to 0·024 mm. (Figs. 26 and 27, *oj*). In the course of the first part of the second parasitic stage the ovijector increases in size, measuring 0·08 to 0·1 mm. in length and 0·03 to 0·035 mm. in width. As this tube increases in size the cells of its wall become flattened and difficult to see and the tube becomes lined with fine longitudinal filaments (Fig. 28, *oj*, Plate XI). Its distal portion at this stage protrudes into the lumen of the vagina like a plug (Fig. 28, *poj*). Toward the end of the second parasitic stage the ovijector increases in length but becomes somewhat constricted and longitudinal folds appear along its inside (Fig. 29, *oj*). At this time a pair of the large cells can be seen at the sides of the posterior end of the ovijector (Fig. 30). These cells gradually become difficult to see, producing some granules. The structures formed from these cells seem to be a fixation apparatus to hold the ovijector in that place, since the posterior end of the ovijector is always found on the ventral side of the intestine, while all other parts of the internal sex-organs remove from the ventral to the dorsal side of the intestine. Therefore the ovijector of the adult worm is found to be more or less twisted, crossing the posterior part of the intestine. It has a well-developed wall, and has a size of 0·1 to 0·13 mm. by 0·025 to 0·03 mm. in living specimens. The wall is thickened at the beginning of the ovijector, forming a sphincter, and its posterior end projects into the vagina like a plug, forming the second part of the ovijector (pars ejectrix of the ovijector). Accordingly the second part of the ovijector (Figs. 28–31, *poj*) is composed of the distal end of the ovijector and the anterior portion of the vagina. The former is inside and shows longitudinal folds, while the latter is outside and is transversely striated.

## (2) The External Sex-Organs.

*General description.* The term "external sex-organs" refers to those organs which have to do with reproduction in the female but do not develop from the genital primordium. They include the posterior part of the ovijector, the vagina, and the vulva.

At the beginning of parasitic life there are many cells in the tail region of the female. These cells gradually increase in size and in number with development. The majority of these cells are not associated in any demonstrable way with the formation of the external sex-organs. In the course of the second parasitic stage, they gradually decrease in number and in size. Only the cells which are situated on the ventral side just in front of the anus are associated with the formation of the external sex-organs. During the second moult these cells increase in number and come into contact with the genital primordium

(Fig. 24, Plate XI). At the completion of the second moult they invaginate and push their way into the genital primordium, dividing it into two parts (Fig. 25, *eso*). The posterior portion of the genital primordium becomes very distinctly separated from its main part by this invagination. It gradually decreases in size with the development of the external sex-organs and finally disappears (Figs. 25–27, *pdr*). The invaginated cells increase in size and number and fuse with the cells of the distal end of the ovijector (Fig. 26). At this time, the cells which form the external sex-organs become arranged in a definite manner and the vagina and vulva become differentiated (Fig. 27).

*The vulva.* Seven to eight cells situated at the entrance of the invagination are high columnar or conical in shape and form a funnel-shaped opening (Figs. 27 and 28, *v*). With the development of the body, these cells gradually become larger and show hook-like projections from their protoplasm (Figs. 28 and 29, *v*). The cells with projections are usually three to four in number on each side of the opening. During the last moult these cells become cuboidal in shape and lose their projections (Fig. 30). At this time there is no opening through the cuticula into the vulva. Just before the last moult is completed the vulva opens through the newly formed cuticula. The new formed skin becomes loose, showing small folds at the entrance to the vulva. After completion of the third ecdysis, the vulva opens directly toward the outside (Fig. 31, *v*, Plate XI). The new formed skin becomes much looser and extends posteriorly, forming a peculiar sac at the posterior end of the female.

*The vagina.* The vagina develops from the invaginated cells mentioned above. When the vagina first becomes differentiated from the vulva it consists of two to three pairs of cuboid cells which connect with the posterior end of the ovijector (Fig. 27, *vg*). In the course of the second parasitic stage the vagina develops gradually, forming a tube, and its anterior end extends a little upward along the distal portion of the ovijector, forming the second part of the ovijector (Fig. 28, *vg* and *poj*). Toward the end of the second parasitic stage, the vagina develops rapidly. The cells in its wall increase in size and are very irregular in shape (Fig. 29, *vg*). They then become flattened and difficult to see, undergoing a granular degeneration. Finally the wall of the vagina appears to be formed of cuticular substance and is transversely striated (Figs. 30 and 31, *vg*). These striations appear first in the second part of the ovijector and then develop along the whole wall of the vagina. Until the completion of the third ecdysis, the vagina and the vulva are clearly distinguished, while in the adult stage they are not separated. Accordingly, the vagina of the adult worms is much longer than that of those in the fourth parasitic stage.

## V. ADULT.

While studying the life-history of *H. muris*, I found some points of adult structure which were overlooked in my previous paper (1920). I will here make them clear.

1. As noted above, the cuticula of the adult worm consists of two separate

layers, the inner one of which has not been observed before. The outer one probably represents an incomplete moult, and is much wider than the inner one. The inner cuticula is thin and has only transverse striations and not the longitudinal ridges which are so prominent on the outer cuticula. These two layers of cuticula are fused at the anterior tip, at the posterior limit of the cephalic inflation, at the anus, vulva and the tail of the female and over the whole of the bursa of the male.

2. The oviduct of the adult female was not distinguished in my first study. However, by the study of the life-history it is made clear, measuring about 0·07 to 0·09 mm. in length.

3. The structure of the second part of the ovijector (pars ejectrix of the ovijector) was not clearly understood before. Now I understand its structure by the study of its post-embryonal development.

## VI. SUMMARY.

1. *Heligmosomum muris* proved to be very favourable material for the study of nematode development, since it will develop perfectly normally in culture rats, infection is easily carried out and since sexual maturity is reached in 7–10 days after infection.

2. The post-embryonal development of *H. muris* is divided into five stages, two free and three parasitic, with three moults. There is only one moult during free life, the second and third stages being separated by change of habitat brought about by entrance into the host. Sexual maturity is attained soon after the completion of the third moult. The mature worm has two cuticular layers, the outer of which is separated by a space from the inner. This outer cuticula is probably the beginning of a fourth moult which is never completed.

3. Under favourable conditions the eggs hatch in about 20 to 24 hours after being passed with the faeces.

4. The first two stages of post-embryonal development, which are passed in free life, are separated by a relatively long moult during which the larva changes from the rhabditiform type to the filariform type. During this period there is a rapid division of the cells lining the intestine, which frees masses of these cells into the lumen and leaves the intestine of the filariform larva lined with flattened cells.

5. The infective stage is not enclosed in a sheath and tends to work its way out of the culture onto the glass or along the edges of the filter paper. At this stage it is impossible to distinguish the sexes.

6. Infection of the rat can be accomplished both by way of the mouth or through the skin although the latter method is by far the most effective. The larvae reach the lungs about 14 to 20 hours after penetration through the skin. They remain in the lungs until about 35 to 65 hours after infection. The majority of them reach the intestine 50 to 65 hours after infection, although in a few they were found as early as 45 hours.

7. In the lungs the larvae increase rapidly in size and moult just before they migrate to the intestine. Early in the development in the lungs the sexes can be distinguished by: (1) the migration toward the posterior end of the genital primordium of the female, (2) structural differences in the caudal region, and (3) differences in shape of the genital primordium.

8. After reaching the intestine the larvae grow rapidly and enter into the third moult from 96 to 108 hours after infection. In the fourth larval stage between the second and third moults growth and differentiation are most marked. It is during this stage that the differentiation of the organs of the reproductive system occurs.

9. Shortly after the completion of the third moult sexual maturity is reached and later the cuticula separates into two layers.

10. During the course of development the changes in size and shape and in the character of the cuticula were traced step by step and the differentiation of the digestive and excretory systems were followed as completely as the material would permit. However it was in following the details of the development of the reproductive organs that the investigation was most fully carried out.

11. In the male reproductive system the testes, vas deferens, seminal vesicle, cement gland and ejaculatory duct arise by differentiations of the genital primordium and are therefore called internal sex-organs, while the bursa and the spicules which are not developed from the genital primordium are known as the external sex-organs.

12. Toward the end of the third larval stage (first parasitic stage) the genital primordium of the male becomes separated into two parts by an extremely delicate strand of tissue. The anterior half of this genital primordium grows forward up to the oesophageal region and forms the testes, the narrow strand connecting the two parts develops into the vas deferens, and the posterior part grows backward to the posterior end, becomes tubular and forms the seminal vesicle, cement gland and ejaculatory duct.

13. The bursa is formed from the walls of the posterior end of the male which become very much inflated, and the spicules develop from secretions of a group of spindle-shaped cells which are early differentiated in the posterior region.

14. In the development of the female reproductive system the ovary, oviduct, seminal receptacle, uterus and the anterior part of the ovijector arise from the differentiation of the genital primordium and are therefore called internal sex-organs, while the vulva, vagina and posterior part of the ovijector arise from invagination and differentiation of subcuticular cells of the posterior end and are therefore called external reproductive organs.

15. After the genital primordium has migrated backward to a position on the ventral side just in front of the anus, it elongates very greatly and grows forward. The anterior part remains as a solid mass of cells and differentiates into the ovary. The rest of the primordium becomes tubular and differentiates into the oviduct, seminal receptacle, uterus and ovijector.

16. A group of cells just in front of the rectum and just over the posterior part of the genital primordium increases in number, invaginates, becomes differentiated into a tube which joins with the posterior part of the genital primordium. This tube differentiates into the vulva and vagina. Where it joins the posterior end of the internal reproductive organs there is an overlapping so that the posterior end of the ovijector has a double origin.

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## DESCRIPTION OF PLATES VII—XII.

All figures were drawn with a camera lucida from living material.

### ABBREVIATIONS USED.

*agp*, anterior part of genital primordium of male; *bc*, buccal-cavity; *bs*, bursal space; *cg*, cervical gland cell; *cg*, cervical glands; *cmg*, cement gland; *cs*, cells which form spicules; *dl*, dorsal lobe of bursa; *e*, egg cell; *ed*, ejaculatory duct; *eg*, cells of esophageal glands; *ep*, excretory pore; *ev*, excretory vesicle; *eso*, beginning of external sex-organs; *gp*, genital primordium; *iv*, cells of intestinal valve; *lb*, lateral band; *n*, nerve ring; *ncg*, nuclei of cervical gland; *oej*, opening of ejaculatory duct; *oj*, ovijector; *ov*, oviduct; *ovs*, sphincter of oviduct; *pac*, post-anal cell; *ppa*, pulvillus post-analis; *poj*, posterior division of ovijector; *peo*, posterior end of ovary; *pdr*, posterior degenerating region of genital primordium; *pgp*, posterior part of genital primordium of male; *pwc*, posterior wall of cloaca; *r*, rectum; *rc*, cells of rectal ligament or sphincter; *rm*, rectal membrane; *rms*, retractor muscles of spicules; *rs*, space surrounding rectum; *s*, spicules; *sr*, seminal receptacle; *sv*, seminal vesicle; *t*, testis; *u*, uterus; *v*, vulva; *vd*, vas deferens; *vg*, vagina.

### PLATE VII.

Fig. 1. Rhabditiform larva just after hatching, 15 hours after culturing in liquid medium.

Fig. 2. Rhabditiform larva, partly developed, two days after culturing in liquid medium.

Fig. 3. Full grown rhabditiform larva, just before first moult, with cells of the intestinal wall beginning to divide.

Fig. 4. Larva preparing for the first moult, division and degeneration of outer layer of intestinal cells complete.

## PLATE VIII.

Fig. 5. Filariform larva, just before casting of the cuticula in the first moult.
Fig. 6. Mature filariform larva in infective stage.
Fig. 7. Larva in the first parasitic stage, 23 hours after infection in the lung of experimental rat.

## PLATE IX.

Figs. 8–16 of Plate IX and Figs. 19 and 21 of Plate X show the development of the external sex-organs—bursa, spicules, etc.—of the male.

Fig. 8. Posterior end of male in the first parasitic stage 23 hours after infection.
Fig. 9. Posterior end of male in the first parasitic stage 30 hours after infection.
Fig. 10. Posterior end of male in the first parasitic stage 40 hours after infection.
Fig. 11. Posterior end of male during the second moult 48 hours after infection.
Fig. 12. Posterior end of male in the beginning of the second parasitic stage, 62 hours after infection.
Fig. 13. Posterior end of male in the second parasitic stage 70 hours after infection.
Fig. 14. Posterior end of male in the second parasitic stage 80 hours after infection.
Fig. 15. Posterior end of male in the second parasitic stage 90 hours after infection.

Figs. 8–15 represent optical sections through the middle of the posterior end of the males.

Fig. 16. Surface view of posterior end of male in the second parasitic stage 90 hours after infection.
Fig. 17. A portion of the body of a male, 60 hours after infection, showing the genital primordium divided into two distinct parts.

## PLATE X.

Fig. 18. Male in the second parasitic stage 72 hours after infection.
Fig. 19. Posterior region of male in the second parasitic stage, 96 hours after infection.
Fig. 20. A portion of the body of a male, 108 hours after infection, showing the development of the vas deferens, seminal vesicle and cement glands.
Fig. 21. Posterior end of male at the beginning of third parasitic stage 120 hours after infection.

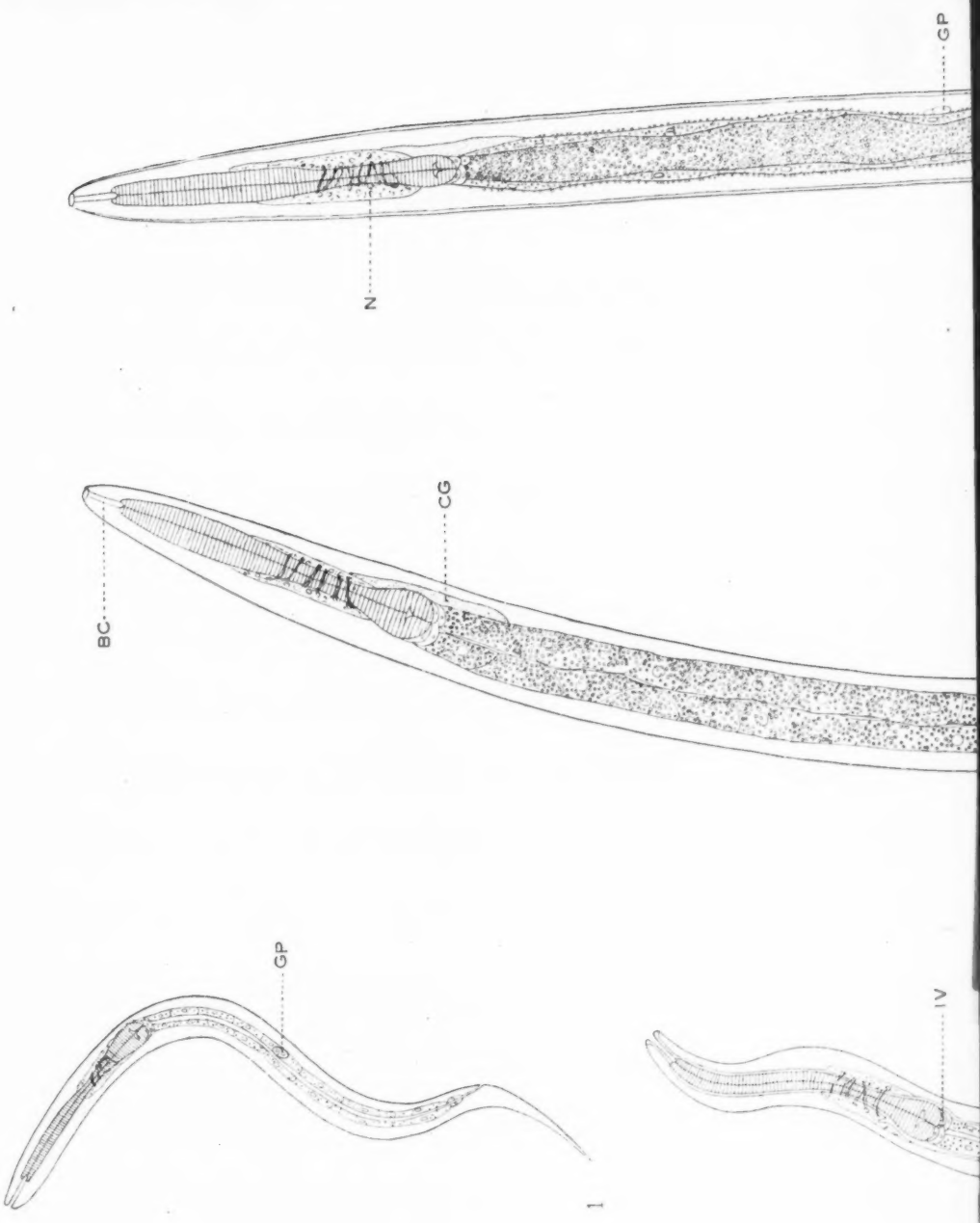
## PLATE XI.

Figs. 22–31 show the development of the external reproductive organs of the female.

Fig. 22. Posterior end of female in the first parasitic stage 23 hours after infection.
Fig. 23. Posterior end of female in the first parasitic stage 35 hours after infection.
Fig. 24. Posterior end of female during the second moult 48 hours after infection.
Fig. 25. Posterior end of female at beginning of the second parasitic stage 55 hours after infection.
Fig. 26. Posterior end of female in the second parasitic stage 60 hours after infection.
Fig. 27. Posterior end of female in the second parasitic stage 70 hours after infection.
Fig. 28. Posterior end of female in the second parasitic stage 76 hours after infection.
Fig. 29. Posterior end of female in the second parasitic stage 85 hours after infection.
Fig. 30. Posterior end of female during the third moult 100 hours after infection.
Fig. 31. Posterior end of female at the beginning of the third parasitic stage 120 hours after infection.

## PLATE XII.

Fig. 32. A small portion of the body of a female in the second parasitic stage 82 hours after infection showing part of the ovary and seminal receptacle.
Fig. 33. A portion of the body of a female in the second parasitic stage 120 hours after infection showing the formation of the oviduct.
Fig. 34. A portion of the body of a female in the second parasitic stage 120 hours after infection showing the oviduct more advanced in development than in Fig. 33.
Fig. 35. A portion of the body of a female in the adult condition 140 hours after infection showing the oviduct.
Fig. 36. Posterior half of the body of a female in the second parasitic stage 85 hours after infection showing the whole reproductive system at this stage.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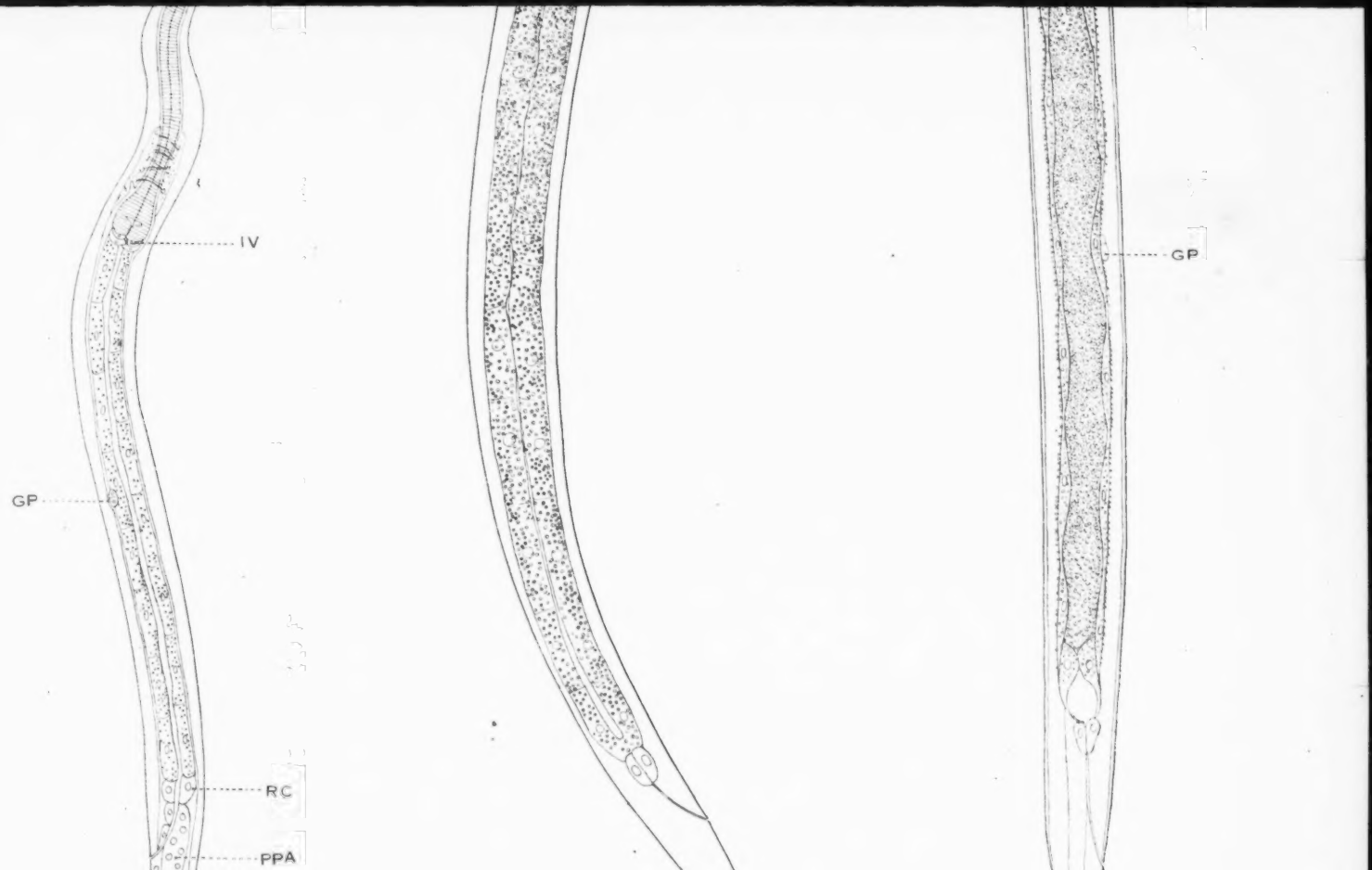
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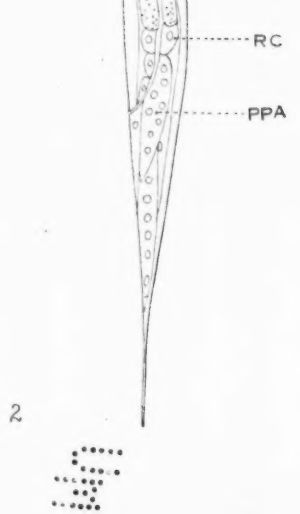


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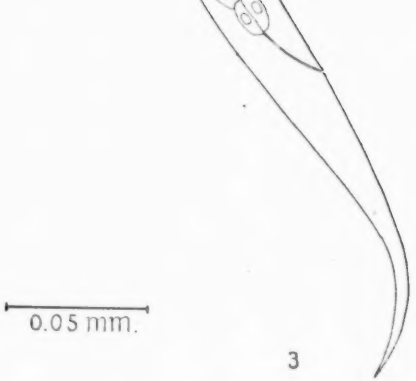


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PLATE VII

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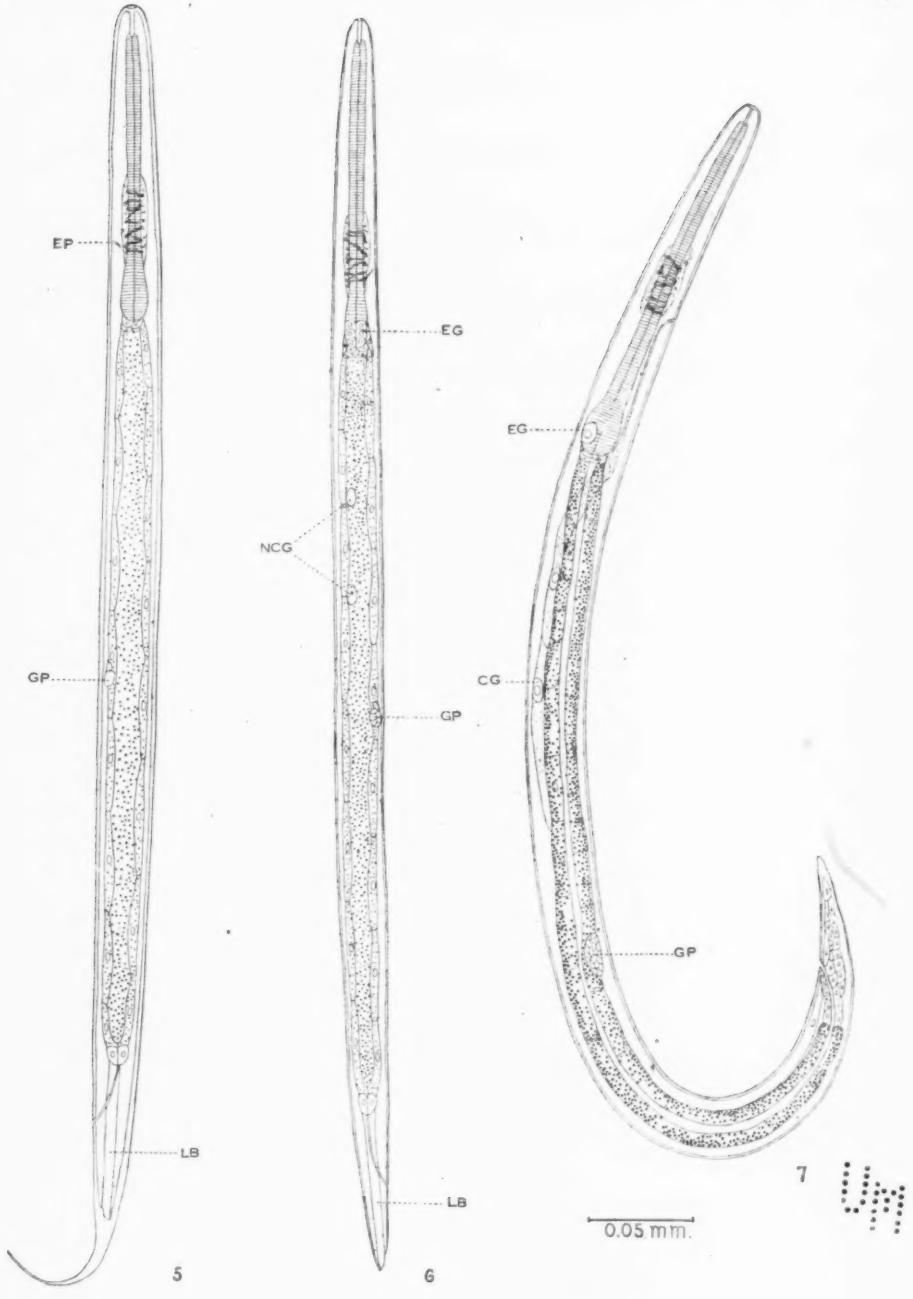
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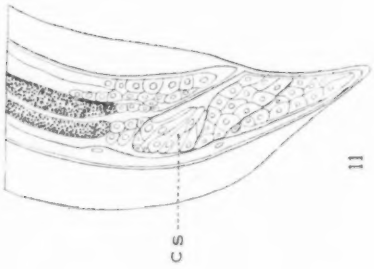


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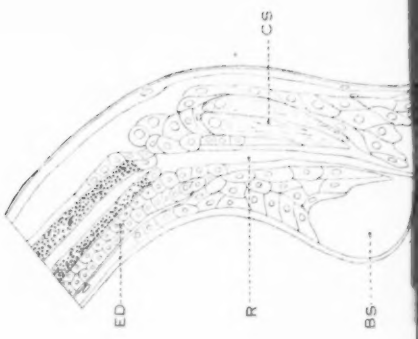


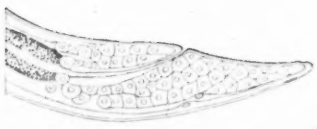

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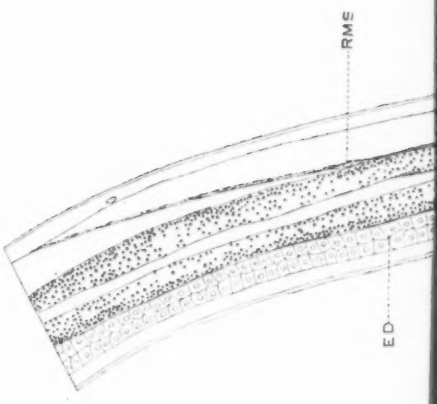


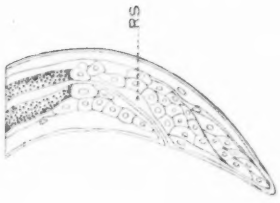


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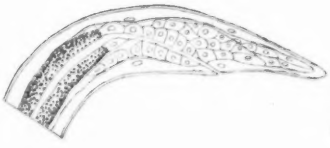

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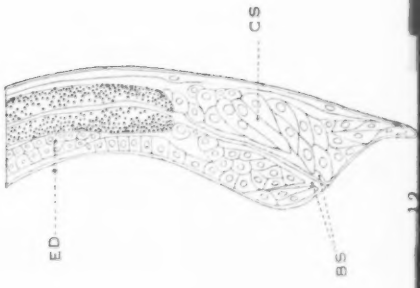


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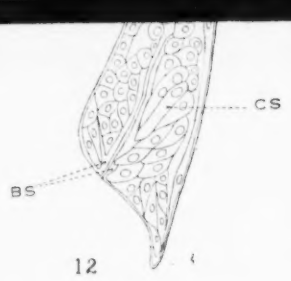


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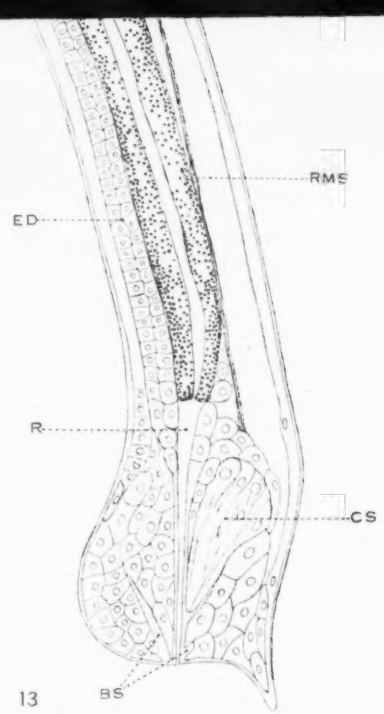


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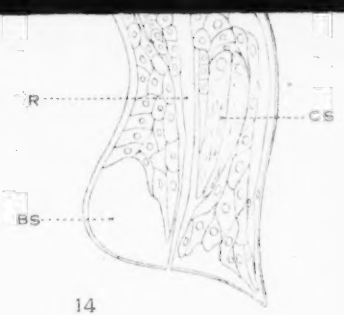


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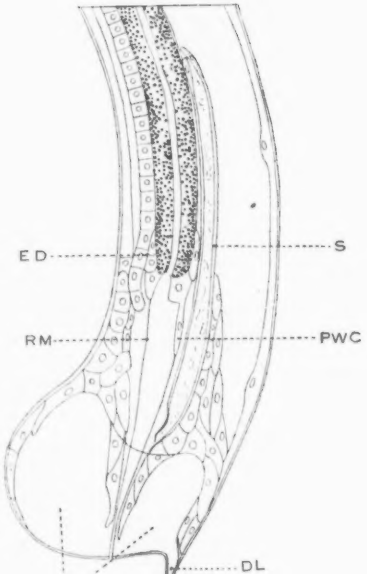

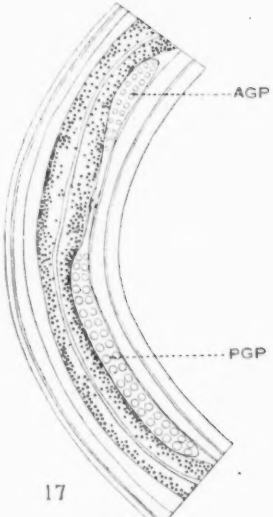


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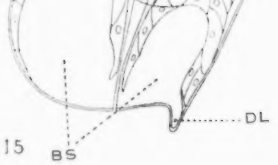


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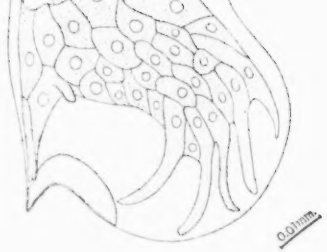


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PLATE IX

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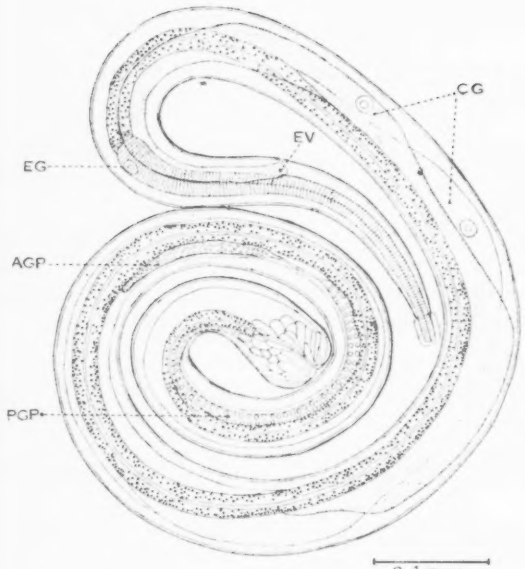
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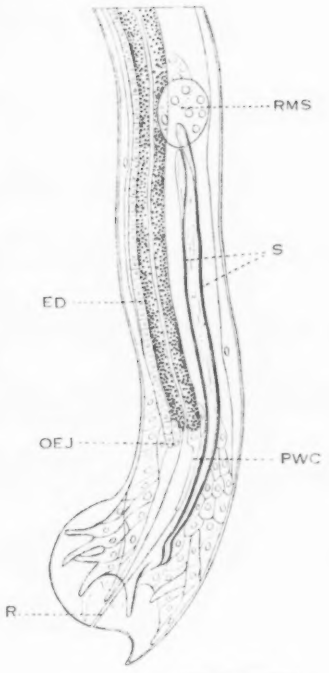
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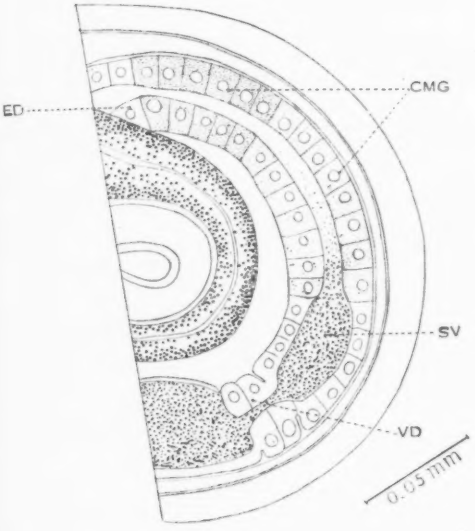
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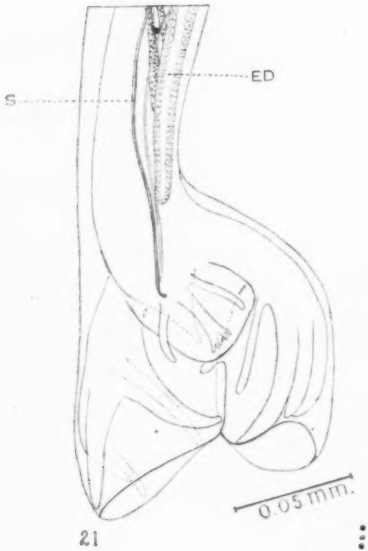
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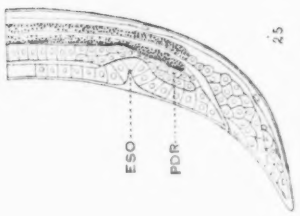


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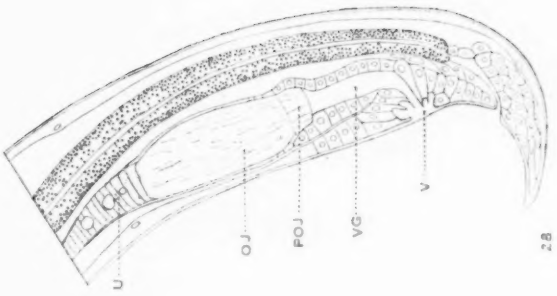


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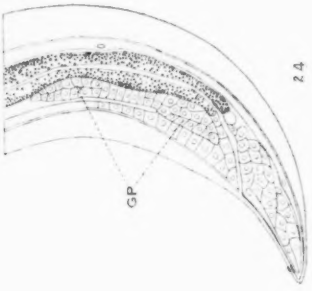


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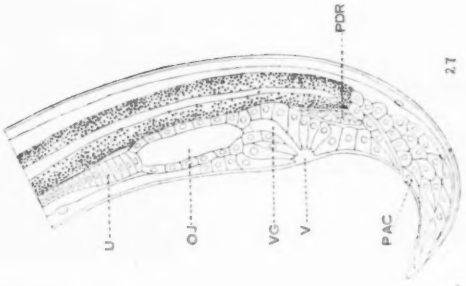


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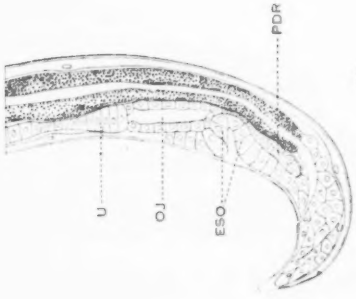


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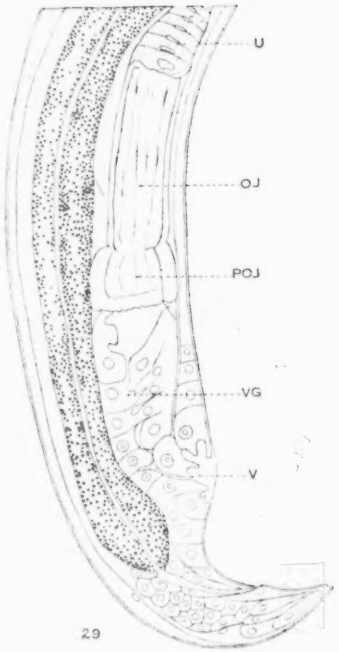


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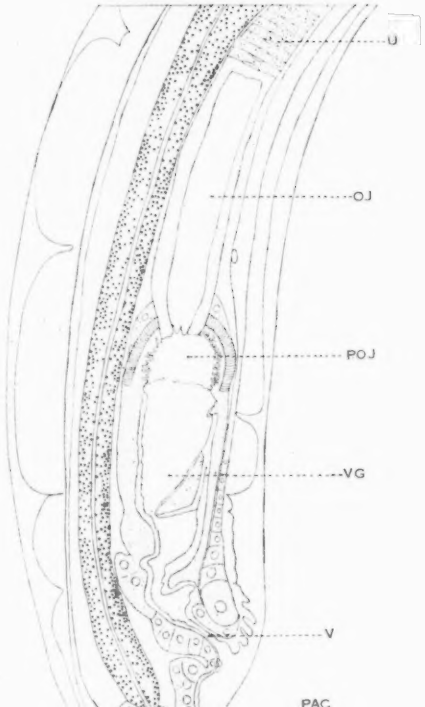


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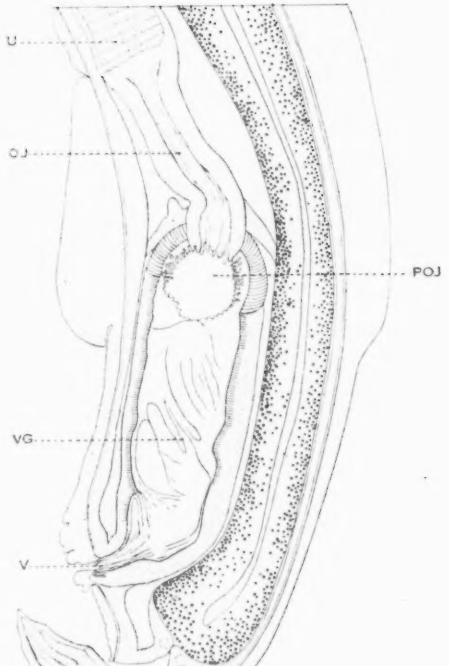
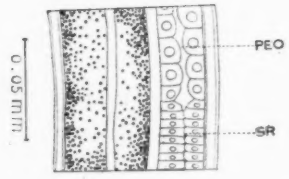


PLATE XI

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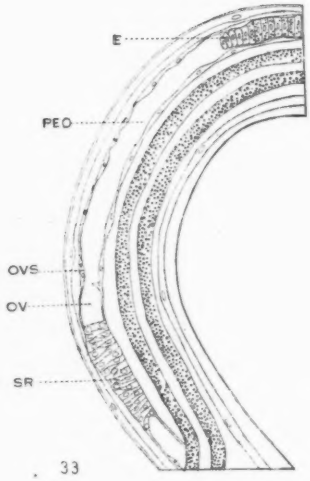


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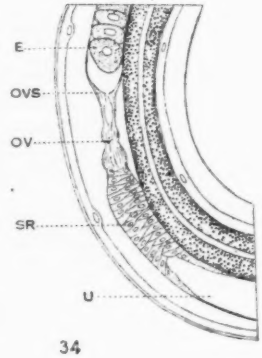


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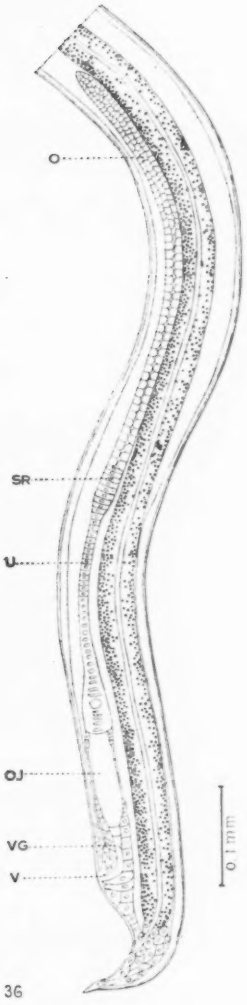


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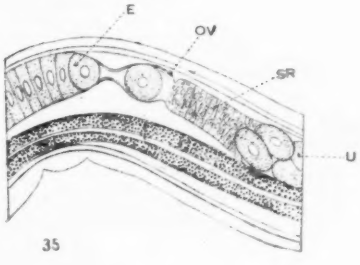



35

# ON THE LARVAL DEVELOPMENT OF *DACNUSA AREOLARIS* NEES (BRACONIDAE), A PARASITE OF PHYTOMYZINAE (DIPTERA), WITH A NOTE ON CERTAIN CHALCID PARASITES OF PHYTOMYZIDS.

By MAUD D. HAVILAND,

*Research Fellow of Newnham College.*

(With 5 Text-figures.)

## INTRODUCTION.

In the summer of 1921, the Wild Angelica (*Angelica campestris*) in the neighbourhood of Cambridge was infested by a leaf-mining fly, *Phytomyza angelicae* Zett. At the end of May and beginning of June, about 60 per cent. of the larvae collected were found to contain an endoparasitic Braconid, *Dacnusa areolaris* Nees. No other internal parasite was present, a fact which simplified working out the development of this form.

I must express my best thanks to Prof. J. Stanley Gardiner, who gave me facilities for carrying out the work in the Zoological Laboratory at Cambridge; and my obligations to Messrs J. E. Collin and G. T. Lyle, who kindly identified examples of host and parasite respectively.

## NOTE ON THE BIOLOGY OF THE HOST.

The larva of *Phytomyza angelicae* mines into the leaves of *Angelica campestris*, forming irregular discoloured blisters on their surface. Usually each mine contains a single larva, but occasionally, when the blisters become confluent, two or three larvae may be found together. When fully fed, the larva leaves the leaf by a slit on the undersurface of the blister, and falls to the ground where it pupates. The imagos usually emerge 19–20 days later, but the pupal period may be prolonged up to 25 days.

In captivity, pairing and oviposition took place a few hours after emergence, and the flies lived only one or two days.

## THE DEVELOPMENT OF THE PARASITE.

The Phytomyzid is liable to attack by *D. areolaris* only in the earliest larval stages, when less than 0·5 mm. in length, and older larvae seem to be immune.

When introduced into a tube with suitable material, the female Braconid eagerly explored the upper surface of the leaf until she located a suitable host

under the epidermis. The actual insertion of the egg apparently presented some difficulties, and the ovipositor was half inserted and withdrawn many times. Occasionally two parasites attacked the same larva, and jostled and thrust each other aside in their efforts to oviposit. If the blister was cut open, the Braconid would sometimes slip inside it, but in such cases she ignored the object of her search which lay exposed before her, and ran out again immediately to probe for it through the epidermis.

Larvae which had already been parasitised were never attacked, and in the considerable quantity of material examined two parasites were never found in the same host. Epiparasitism[1] (double infestation) does not seem to occur in this species.

The egg, when first laid, is an oval body somewhat pointed at the anterior end (Fig. 1); but, as segmentation proceeds, it increases in size and becomes more spherical. It lies freely in the haemocoele, generally in the posterior third of the body, but occasionally may be found near the head. The material available was insufficient for the study of the embryology of the parasite. The earliest larval stage, which appeared in every larva found parasitised in the field, is that shown in Fig. 2. The larva, transparent and vermiform, lies slightly curved to the ventral side, in the cavity of a hollow sphere of flattened cells, the "trophic membrane," which completely envelopes it. The body consists of thirteen segments, each of which from the second to the twelfth bears dorsally a few short spines. The thirteenth segment, which is blunt and rounded, is provided with a semicircle of stouter setae, arranged fanwise round the anus. The larva is able to move about within the trophic membrane. The cells of the latter, though polygonal in surface view, are flattened and crescentic in section, and towards the end of embryonic development their nuclei appear in various stages of degeneration. This cellular sphere is enclosed in a fine structureless membrane.

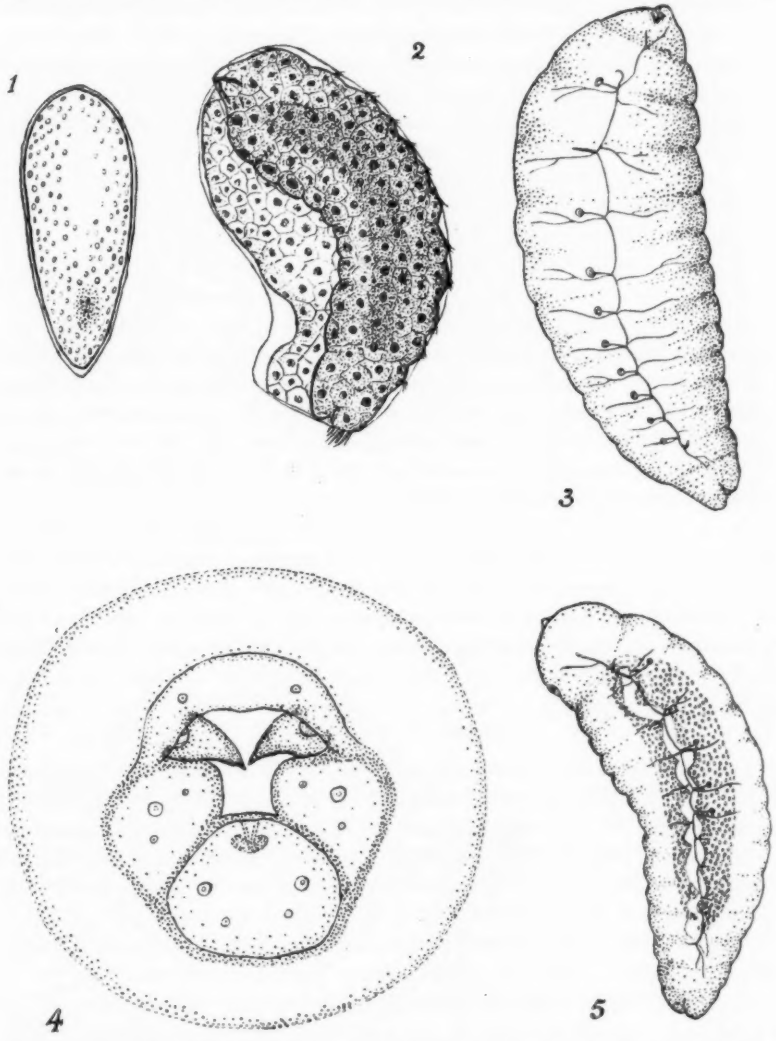
In this condition the parasite remains until the host larva is fully fed and falls from the leaf. Examples examined twelve hours after this event show some increase in the size of the parasite, which half fills the cavity of the membrane. The latter becomes attenuated and is pierced by the dorsal and caudal spines. It ultimately ruptures in the region of the mouth of the parasite, which now begins to feed, and the mesenteron, filled with ingested matter, is clearly visible through the transparent tissues.

About 36 hours after the host has formed its puparium, the parasite throws off the trophic membrane, and with it the first larval skin, both of which soon disappear among the surrounding histolysed tissues.

In the succeeding stages the parasite larva is a semi-transparent, smooth, apodous form, slightly curved to the ventral side, and without appendages. As it feeds it increases rapidly in size, and, about a week after the first moult, having demolished the viscera of the Phytomyzid, it comes forth from the empty skin and lies free within the puparium.

[1] The writer first suggested and defined this term (1922) in *Proc. Camb. Philos. Soc.* XXI. 27.

The fully-fed larva is creamy, white and opaque, with a cuticle studded with minute scales or spines. The mandibles are small, blunt and unidentate.




*Dacnusa areolaris* Nees. Fig. 1. The egg at oviposition. ×350. Fig. 2. The larva shortly before rupture of the trophic membrane. ×100. Fig. 3. The full grown larva. ×30. Fig. 4. Buccal armature of the full grown larva. ×350.

Young *Eulophinid* larva. Fig. 5. ×150.

The labrum, which projects prominently, bears two pairs of papillae. Three similar processes occur on each maxilla, and the labrum is likewise furnished

with a pair. There are now nine pairs of open spiracles on segments 2, 4–11, and, in addition, a closed spiracular trunk on segment 3 (Fig. 3).

The internal structure approximates closely to the type of hymenopterous larvae in general, and calls for no particular comment.

*Dacnusa areolaris* undergoes metamorphosis within the host's puparium, and no cocoon is woven. The period of pupation is usually about two weeks. The development of the parasite is however very closely correlated with that of the host, as may be seen by the accompanying table:

| Pupation of host | Emergence of host | Emergence of parasite |
|---|---|---|
| June 1 | June 24–25 | June 25–27 |
| „ 5 | „ 25–26 | „ 26–27 |
| „ 7 | „ 26 | „ 26 |
| „ 10 | July 1 | July 1 |

All the puparia collected on one day were set apart, and the emergences of hosts and parasites noted separately. It will be seen that the development of the parasite from the first moult to the emergence of the imago is one or two days longer than the puparial period of the host. In the first collection, where the host's emergence was delayed for five days, the emergence of the parasite was correspondingly deferred.

The imagos lived for five or six days in captivity, when fed on sugar and water. It is possible that this is a further correlation between parasite and host, for, as previously remarked, the life of the latter is short, and oviposition takes place soon after emergence. In parasitised populations, the flies thus emerge and oviposit a day or two before the Braconids appear. Hence there will be a sufficiency of hosts by the time the parasites are ready to deposit their eggs.

## GENERAL REMARKS.

The genus *Dacnusa* was named by Haliday in 1839, although certain of the species now included in it were described earlier by Nees von Esenbeck. Marshall (1885) in his Monograph describes 29 forms, but he remarks that some of these are ill-defined, and that their systematic position requires further investigation. The species whose hosts are known have all been reared from Phytomyzid or Agromyzid larvae.

Other Braconidae whose life cycles have been described include a few species which are endoparasitic in dipterous larvae.

Keilin and Picado (1913) published an account of the larval forms of *Diachasma crawfordi*, parasitic on the fruit fly *Anastrepha striata* Shin.

Pluvinel (1914) observed the development of *Adelura gahani*, a parasite of a Phytomyzid.

Alston (1920), in a detailed bionomical study, described the larva of *Alysia manducator* Panz., a parasite of the blow-fly.

The larva of *D. areolaris*, with its trophic membrane, much resembles that of the Chalcid, *Smicra clavipes*, figured by Henneguy (1892), and endoparasitic

in *Stratiomys strigosa*. In comparing the present species with the Braconidae-Flessiliventres, such as *Aphidius*, in which a trophic membrane is also formed round the embryo, there appears to be a tendency to lengthen embryonic at the expense of larval development. Thus in *Aphidius*, the membrane is cast off early, and the caudate larva moults twice before assuming the typical grub-shaped form; whereas in *D. areolaris* the larva begins to ingest food while still within the membrane, and after throwing off the latter and the first larval skin together, it at once appears in the typical form. Fig. 2 shows the only stage found in a large number of Phytomyzid larvae of all ages which were examined; and this suggests that, as the parasite oviposits when the host is very young, development before the metamorphosis of the latter does not proceed beyond a certain limit, although there is some increase in the size of the embryo, proportionate to the growth of the host.

This adaptation may be correlated with the very complete metamorphosis of the host. In the early stages, the only nourishment taken is that which transfuses through the trophic membrane, but when the host forms its puparium, the parasite begins to ingest the surrounding tissues, and the mid-gut is filled with food. The mandibles of the hymenopterous parasites are better adapted for prehension than for mastication; and *Aphidius* and others break down the host's tissues by a kind of "external digestion." But if parasites of holometabolous insects can in any way delay growth until the metamorphosis of the host takes place, the organs of the latter will of themselves disintegrate and undergo profound physical and chemical changes, providing what is presumably a suitable pabulum for the further development of the parasite. Unfortunately the literature of insect parasitism throws little light on this subject, but it has been suggested by me elsewhere (1921) that the early form of *Charips*, a Cynipid endoparasite of *Aphidius*, may be a kind of resting stage.

It is obvious that it would be to the advantage of the parasite that the host should attain the full size before death or metamorphosis, in order that plenty of food should be available for its own subsequent development. The ectoparasitic Chalcids mentioned below probably rely partly on bacterial action for the disintegration of their food, and begin to feed immediately after hatching, no matter what the size of the host may be. As a result, there is considerable diversity of size of the imagos, and this may be suggested as the cause of the occasional disability of the parasite to complete its transformation.

This diversity of size, owing to variability of nutrition, may lead to far-reaching results.

Keilin (1915) observed that the size of the imagos of *Pollenia rudis* Fab. is determined by the dimensions of the host, or by its accidental death before the parasite larva is full fed; and he points out that if the difference in size should make mating impossible between large and small forms, distinct races might arise within the species. He cites the observations of Pantel, according to which the Tachinid, *Meigenia floralis*, typically a parasite of *Crioceris*

(Coleoptera), occasionally attacks another and larger larva of the same group (? *Timarcha*). The flies bred from the latter host are so much larger than the type, that they have been described as a variety, *Meigenia floralis* var. *major*. Inversely, examples of *Thrixion halidaynum*, reared from a small phasmid, are smaller than the type, which is parasitic upon a larger species of the same genus.

This segregation could become permanent only if one form is structurally or physiologically compelled to oviposit in a host resembling that from which it was itself reared. Otherwise its offspring would revert to the grand-parental type.

In the *Phytomyza* + *Dacnusa* complex, the correlation between the cessation of growth and metamorphosis of the host, and the inauguration of post-embryonic development of the parasite, insures not only that the latter shall be provided with sufficient food to carry it through its transformation, but also that the imago shall approximate to the mean size of the race.

## NOTE ON CHALCID PARASITES OF *PHYTOMYZA ANGELICAE*.

At the beginning of August, collections of *Phytomyza angelicae* showed that while there was still considerable infestation by *D. areolaris*, 80 per cent. of the fly larvae had been parasitised or epiparasitised, as the case might be, by certain ectoparasitic Chalcids. Dr Luigi Massi of Genoa kindly examined examples of the three forms obtained, and referred them to the genera *Chrysocharis*, *Eulophus* or *Hemitarsus* of the sub-family Eulophinae, some of which are known to be parasites of Phytomyzinae.

The larvae feed externally upon the host, and are of the usual type of Chalcid larva. The body is 13 segmented, and the head is furnished with two tactile processes. At first there are four pairs of open spiracles, but when fully fed there are nine, namely on segments 2–10 (Fig. 5).

As development proceeds, the larvae increase in size, but do not change materially in form. The host dies soon after the parasite has begun to feed, and in five or six days only the empty skin is left, together with the calcospherites, or crystalloid concretions of certain cells of the fat body. These Chalcids weave no cocoon, but undergo metamorphosis within the blister on the leaf. The pupal period is about four weeks.

## SUMMARY.

1. *Dacnusa areolaris* Nees is a parasite of the fly *Phytomyza angelicae* Zett.

2. The egg is laid and development takes place within the body of the host.

3. A membrane of trophic cells is formed, within which the embryonic and first larval stages are passed.

4. The further growth and development of the parasite are delayed until after metamorphosis of the host, probably to ensure sufficient food in the later stages.

5. The length of the larval and pupal life of the parasite is intimately correlated with the puparial period of the host.

6. It is suggested that this is an adaptation to ensure that an adequate supply of host larvae shall be hatched by the time that the parasites are ready to oviposit.

7. Certain Chalcididae of the genera *Eulophus* and *Chrysocharis* are ecto-parasites of *Ph. angelicae*, and a summary of observations on their life cycle is given.

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# NOTES BEARING ON DUFOUR, VON SIEBOLD AND GOODSIR, WHOSE PORTRAITS APPEAR IN *PARASITOLOGY*, XIV, No. 2.

## PORTRAIT-PLATES XV—XVII.

(Continuing the series begun in Vol. XIII.)

BY GEORGE H. F. NUTTALL, F.R.S.

(*From the Molteno Institute for Research in Parasitology.*)

### Jean-Marie-Léon Dufour.

1780–1865.

(Portrait-plate XV.)

LÉON DUFOUR was born 11 April, 1780, at Saint Sever (Landes) and died there 18 April, 1865. He was a medical man and a naturalist. He took his M.D. at Montpellier in 1806. From 1806 to 1814 he served in the army, then turned his attention to entomology and botany, but in 1823 he took part in the Spanish Campaign as an army doctor. He distinguished himself especially through his work on the anatomy and physiology of arthropods and upon the habits and metamorphosis of insects, but he also wrote on botany, agriculture and meteorology. He was elected to the Academie des Sciences and was the first Frenchman upon whom that body conferred the Cuvier Prize (1861). During 1811–1864 he published 232 papers on entomology, the relation of insects to plant diseases, parasites of Insects, parasitism, Protozoa and Helminths.

His parasitological papers relate to *Ascaris lumbricoides*, *Hippobosca equina* (1825) and *H. camelina* n.sp. (1858), *Ornithomyia biloba* n.sp. (1827–1845), parasitic insect larvae (1828), *Gregarina ovata* n.g., n.sp. (described as a "worm" in the insect's gut, 1828), *Nycteribia* (1831), *Pteroptes vespertilionis* n.sp. (1832, a mite), Nematodes and Gregarines parasitic in Orthoptera and Hymenoptera (1836–7), *Cecidomyia* spp. parasitic on briars, various gall-producing insects (1837–64), *Ceratopogon* (1845), parasitism (1851), flea cocoons (1861).

For Biography see *La Grande Encyclopédie* (Paris), XV. 14; Vapereau's *Dictionnaire des Contemporains* (Paris, 1865), p. 562, from which sources I have drawn; Albertus (1888), Un médecin naturaliste en province, Léon Dufour (Paris), *Gaz. Méd. de Paris* (1888), 7 s. v. 157 *et seq.*; Caffe's Nécrologie in *Journ. d. conn. méd. prat.* (Paris, 1865), XXXII. 205, also "Un Savant," etc. written by his sons (1884–6), *Gaz. d. Hôp. Paris*, LVII–LIX (very lengthy,

abstracted by Albertus, *v. supra*). For Bibliography see *Ann. Soc. Entomol. France*, 1865, 4 s. v. 216 *et seq.* (carefully compiled and annotated by Laboulbène), this volume contains the portrait we reproduce; *Catal. de la Bibl. Nationale*, Paris; Stiles and Hassall's *Index Catal. of Med. and Veter. Zool.*; *Index Catal. Libr. Surg.-Gen.* Washington (chiefly medical). I am indebted to Prof. Bouvier of the Nat. Hist. Mus. Paris for a fine lithographed portrait which unfortunately did not give good results when we sought to reproduce it, this portrait hangs in the Molteno Institute.

## Carl Theodor Ernst von Siebold.

1804–1885.

(Portrait-plate XVI.)

CARL VON SIEBOLD was born 16 February, 1804, at Würzburg, and died 7 April, 1885, in Munich. He belonged to a family of whose members a number were distinguished medical men. He matriculated at Berlin as a medical student in 1823, studied also in Göttingen (1824–27) and in 1828 took his M.D. in Berlin, where he fell under the influence of Rudolphi and Ehrenberg. He practised medicine for some years at Heilsberg, East Prussia, whence he proceeded to Danzig where he spent six years (1834–40) and devoted much of his time to zoological studies and the collection of Insects and Helminths. In 1836 he discovered ciliated epithelium in man when examining an extirpated nasal polyp. He studied the biology of a variety of animals, including Gregarines and Helminths. In 1840 he was called to Erlangen as Professor of Zoology, Comparative Anatomy and Veterinary Medicine. In the article "Parasites" in R. Wagner's *Handwörterbuch* (1844) he writes of Cestodes and Cystici being stages in the life-history of one animal as exemplified in the case of *Taenia crassicollis* of the cat and *Cysticercus fasciolaris* of rodents. In the first part of his *Lehrbuch* (1845) he established the class *Protozoa* which he distinguished as unicellular animals; this book was subsequently translated into French (1849) and English (1854). In 1845–49 he was Professor of Zoology, Comparative Anatomy, Physiology, and Special Physiology at Freiburg, where, with Albert von Kölliker, he founded the *Zeitschrift für wissenschaftliche Zoologie* (1848). He succeeded Purkinje as Professor of Physiology and Director of the Physiological Institute in Breslau but remained there only a few years (1850–53) before he finally attained a suitable goal by proceeding to Munich. Here he taught Physiology and Comparative Anatomy as professor until in 1856 his chair of zoology was established. Whilst in Breslau, following the initial lead of Küchenmeister into the field of experimental helminthology, von Siebold, beginning in 1852, carried out extensive feeding experiments which showed that *Cysticercus* and *Echinococcus* gave rise to Cestodes in animals fed with them; his work on the subject was finally brought together in his publication *Ueber die Bandwürmer und Blasenwürmer* (Munich, 1854), wherein he cites Haubner and Leuckart as having proved the converse,

namely, that Cestodes give rise to *Echinococcus* and *Cysticercus*. In Munich he published a number of papers on parthenogenesis and general zoological subjects but retained his interest in parasitology, at times reverting to matters of which he had treated long before: *Syngamus trachealis* (1835, 1867), Nematodes in insects (1842–58), *Mermis*, *Gordius*, etc. (1845, 1856), Cestodes, *Echinorhynchus* and the parasitic insects *Ornithobia* (1845) and *Liptotena* (1845, 1850), *Pentastomum* (1856). His laboratory facilities in Munich were poor, this doubtless leading to his devoting much time to museum work which checked his original scientific activities and in the opinion of his biographer, Ehlers, proved the truth of Schiödte's criticism of Claparède that "Les musées pèsent lourdement sur la science."

The work of von Siebold, whilst not highly original, was marked by painstaking industry, minute care and sound critical judgment. He laid stress on the need of studying the living animal and in this respect his work recalls that of Spallanzani, Réaumur or de Geer. Among his pupils were Theodore Bilharz, Ferdinand Cohn, Ernst Ehlers and Elie Metchnikoff, to mention but a few. He was the recipient of many honours which will be found enumerated in the *Almanach d. baier. Akad. Wiss.* 1884, p. 130.

For Biography [herein abstracted] see Ehlers (1885), *Zeitschr. f. wiss. Zool.* XLII, pp. i–xxiii, with Bibliography pp. xxiv–xxxiv and heliogravure *portrait* [1868, herein reproduced]. The foregoing bibliography comprises 197 numbers of publications on medical and zoological subjects which appeared in 1828–82. *Portraits*: pencil drawing by von Kaulbach (obtainable in photographic reproduction); painting by von Lenbach; bust by Haller; heliogravure from a photograph by Hanfstängel (1860) in *Zeitschr. f. wiss. Zool.* 1860.

## John Goodsir.

1814–1867.

(Portrait-plate XVII.)

JOHN GOODSIR, the anatomist, was born 20 March, 1814, at Anstruther, Fifeshire, and died 6 March, 1867, of spinal disease in Edinburgh, where he lies buried beside his friend Edward Forbes (1815–54) in the Dean Cemetery[1]. He studied at St Andrews and matriculated at Edinburgh (1830) where he became a Licentiate of the Royal College of Surgeons in 1835, Curator of the Museum of the College (1841) and afterwards (1844) Demonstrator of Anatomy. He became Professor of Anatomy at Edinburgh (1846–1867) and was elected Fellow of the Royal Society.

The value of his original work was widely recognized, a striking tribute being that of Rudolf Virchow who dedicated the first edition of his *Cellular Pathology* (1859) to Goodsir "as one of the earliest and most acute observers of cell-life both physiological and pathological." Goodsir wrote on the develop-

[1] A granite obelisk erected on the spot was engraved with a curved line symbolic of "the law of the vital force."

LÉON DUFOUR

1780—1865

CARL VON SIEBOLD

1804—1885

JOHN GOODSIR

1814—1867

ment of teeth (1839) and for a period worked as a dentist; he also wrote on embryology and zoology.

His discovery of *Sarcina ventriculi* (1842) aroused much interest in the medical world; he founded the genus and species on material obtained from a case of pyrosis or "waterbrash" lasting nearly two months in a youth of 19. He practically cured the case by altered diet, exercise, and creosote per os which checked the fermentation in the stomach. He wrote but few papers on helminthology (*Distomum hepaticum, Gymnorhynchus horridus* Goodsir (1841) and various Cestodes (1844)), and studied potato blight (1846).

For Biography see (1868) *The Anatomical Memoirs of John Goodsir*, edited by W. Turner with a biographical memoir by H. Lonsdale, 2 vols, xxviii + 524 pp., 14 pls., 24 figs., 8vo with *portrait* (herein reproduced), Edinburgh. The biography in *Dict. National Biogr.* XXII is taken from the foregoing. See also Balfour, J. H. (1866–7), *Trans. Botan. Soc. Edin.* IX. 118–127; (1867–8), *Proc. Roy. Soc.* XVI, pp. xiv–xvi; *Edinburgh Med. Journ.* 1867; Cleland, J. (1889), *Memoirs*, etc. London and Edinburgh, 8vo. p. 159 with *portrait*.

His parasitological papers are as follows: History of a case in which a fluid periodically ejected from the stomach contained vegetable organisms [*Sarcina ventriculi*] of an undescribed form, with a chemical analysis of the fluid by George Wilson, *Edin. Med. and Surg. Journ.* LVII [republished 1868 in *Memoirs*, II. 531–371, *v. supra*].

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# A CONTRIBUTION TO THE KNOWLEDGE OF THE *HIPPOBOSCIDAE* (DIPTERA PUPIPARA).

By G. F. FERRIS, M.A. and F. R. COLE, M.A.,
*Stanford University, California.*

(With 20 Text-figures.)

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## Introduction.

The approach to the study of the ectoparasitic flies of the pupiparous family *Hippoboscidae* has heretofore been almost entirely by way of the conventional methods of the Dipterists. In other words, descriptions have been based almost exclusively upon pinned specimens. Consequently these descriptions have, for the most part, considered only the conventional subjects of colour, wing venation, size, shape, form of the claws and a few of the more obvious chaetotactic characters. A few descriptions have been based upon alcoholic specimens and these descriptions are decidedly better than those based upon pinned specimens, although they still leave something to be desired.

It is probable that the greater part of the specimens of Hippoboscids in collections are of the pinned type and it is the belief of the present writers that however satisfactory such specimens may be in the case of representatives of the other families of Diptera they are not adequate for the proper study of the Pupipara. In nearly all the members of this group the abdomen is so soft that it becomes greatly shrivelled in pinned specimens and practically none

of its characters can definitely be determined. A review of the existing descriptions shows that in almost all cases this portion of the body has been passed over with little or no mention. Yet an examination of the material available to us has shown that the abdomen frequently presents characters that we believe to be of very great usefulness.

We are consequently presenting this paper more as a contribution to the methodology of the study of the *Hippoboscidae* than for any other reason, although in its inception it was intended merely for the description of a few new and little known species. We are taking advantage of the opportunity to figure and give notes upon all the species that are available to us for study.

## Technique.

In the course of its development the study of practically all the ectoparasitic groups of insects has passed through certain fairly well-defined stages. Beginning with pinned material, even in those groups the members of which are the most fragile, it has progressed through various types of inadequate preparations resulting finally in the development of a specialized technique for the production of microscopic preparations in the making of which a considerable degree of care and skill is necessary.

In the preparation of slide mounts of Hippoboscids we have utilized the following procedure. In the case of winged specimens the wings are detached and mounted directly. The body is boiled in a 10 per cent. solution of caustic potash until the contents are entirely liquefied. It is then transferred to water, judiciously placed slits are made in it and the contents carefully pressed out. In the case of these insects this is a bit difficult because of the highly developed network of tracheae within the body. The specimen is then transferred to 95 per cent. alcohol for a few minutes, then to carbol-xylene and then mounted in balsam. In most cases it is desirable to support the cover-glass on bits of broken glass in order to avoid distortion of the specimen.

There are certain very definite disadvantages in this method. It is rather difficult to avoid the accidental removal of more or less of the vestiture of setae and some distortion of the body is almost inevitable. The development of a certain amount of skill on the part of the preparator, however, will reduce these disadvantages to a minimum. We cannot consider that objections to the method based solely upon the necessity for acquiring this skill and the time consumed are valid. The histologist does not complain of the time spent in acquiring the skill in technique that is necessary for the accomplishment of his aims.

A further objection that the colours of the specimen are lost by this method of preparation is in part valid. However, what we have seen has not led us to accord any special respect to colour as a taxonomic criterion in this group and in any case colour notes can be taken before the specimen is prepared. The general colour, whether light or dark, can be determined well enough from the mounted specimens as can the colour of setae.

### Figures.

Very few illustrations have been employed in describing members of this family and such as have been given have usually been of but little value to the systematist. In fact the majority of the existing figures can only be described as crude. A most gratifying exception to this rule is that of the figures given by Massonat (1909) in an extended paper on the family. Yet even these figures, although they are probably the best that have been given by any author, are not as detailed and careful as is desirable, too little attention having been given, for instance, to the chaetotaxy, which in some genera is a matter of considerable importance.

The figures that we are presenting have for the most part been made from carefully corrected camera lucida sketches. We have endeavoured to put into them all the structures visible in the specimens, but this ideal cannot entirely be realized, it being impossible to show some of the pleural structures of the thorax. We have endeavoured also to attain a degree of accuracy that will at least come within the probable range of variation. All the figures have been checked over by both authors.

In the case of figures that are divided, the left half represents the dorsal aspect, the right half the ventral aspect. We believe that the many advantages of this type of figure far outweigh any possible disadvantages and are sufficient to overcome any possible objections on the ground that the figures are not artistic.

### Acknowledgments.

The material upon which this paper is based has come from various sources. We are especially indebted to Mr E. P. Van Duzee, Curator of Entomology of the California Academy of Sciences, for placing at our disposal the *Hippoboscidae* in the collection of that institution. The Department of Entomology of the University of California, through Prof. S. B. Freeborn, has loaned material of the genus *Lipoptena*. Certain specimens were taken some years ago by the senior author from skins in the collections of the United States National Museum and the Field Columbian Museum and acknowledgments are due to the authorities of these institutions for this privilege. Finally, to Major E. E. Austen, of the British Museum, we are indebted for specimens of *Lipoptena cervi* and *Ornithomyia lagopodis*.

## Genus **Lipoptena** Nitzsch.

The material of this genus that is before us represents five species, one of which is apparently new. In addition to notes on specific characters we are enabled to add also some information concerning the larvae.

### *Specific characters.*

It appears from our material that excellent specific characters are to be found in the genitalia of the males, which can be seen to advantage only in

cleared specimens; in the chaetotaxy of the head and thorax; in the form of the first abdominal sternite and in the form and arrangement of the tergal plates of the abdomen. There is evidently a certain amount of variation in the chaetotaxy but not enough to be especially disturbing. The presence or absence of an apical seta or setae on certain of the tibiae is evidently a valuable specific character in some instances.

The volant individuals, that is those taken before the wings have been dropped, differ so markedly from those that have dropped the wings and become distended by full feeding that at first difficulty was experienced in correlating the two forms. The abdomen in the volant individuals is so small and contracted that the distribution of the setae can not be determined with accuracy. The tergal plates are not entirely defined, the diverging dorsal lines seen in *L. depressa*, for instance, not appearing at all. Reference to the chaetotaxy of the head and thorax, however, has been sufficient to permit the definite placing of all examples of this sort that we have seen.

### *Sexual dimorphism.*

In pinned specimens of the ordinary type it is very difficult to distinguish between the sexes, in fact most authors appear not to have attempted any such distinction. It seems to have been supposed by some that the males retain the wings. Massonat (1909, p. 59) has pointed out that this is a mistake and we are entirely in accord with his views, for, in our material of *L. depressa* and *L. subulata*, both sexes appear without the wings. It is probable that this mistake has arisen simply from a failure to distinguish the sexes. Correlated with this error, some authors appear to have thought that the slender-bodied volant individuals must be males. For example, one such individual received, through the kindness of Major Austen and by him labelled as a male, is in reality a female.

It is true that in the male the abdomen appears never to attain the size that it does in the female, but otherwise there is little but the presence of the genitalia by which to distinguish them, at least in all the species we have examined except *L. cervi*. We have not seen the male of this species, but according to Massonat there is a decided difference in the form and arrangement of the abdominal plates. The external genitalia of the males at the most consist of a pair of small, ventral processes, and in some of the species even these are lacking. The internal structures show very plainly in cleared specimens and permit no possibility of error as to the sex.

### *Larvae.*

Larvae of two species, *L. depressa* and *L. mazamae*, were found within the bodies of females. The number of specimens (one of each species) is not sufficient to permit any extensive study. Nevertheless, certain interesting facts are revealed.

In both of these larvae the posterior portion of the body is heavily chitinized. There are no distinct spiracles, the place of these being taken by a large number of small, pore-like openings which communicate with tracheal branches, the arrangement being somewhat like that of the polypneustic lobes described by Newstead as occurring in the larva of *Glossina*. In the larva of *L. mazamae* (Fig. 2 *A*) these openings are very numerous, are arranged in two general series and appear to occur on both the dorsal and ventral sides of the body. In that of *L. depressa* they appear to be very few and confined to one side of the body, but our single specimen is in too poor condition for study to permit a definite determination of the condition.

### *Lipoptena depressa* (Say).

Figs. 1, 2 *B*, 2 *D*, 2 *F*.

1823. *Melophagus depressus* Say, *Journ. Acad. Sci. Phil.* III. 104.
1907. *Lipoptena depressa* (Say), Coquillet, *Ent. News*, XVIII. 290.

Previous Records. Originally described by Say from *Cervus virginianus*, without indication of locality. This is probably some sub-species of the deer now known as *Odocoileus americanus*, which ranges throughout a large part of North America east of the Rocky Mountains. Recorded by Coquillet from "black tailed deer" (*Odocoileus columbianus*) from Humboldt County, California.

Speiser has placed *L. mazamae* Rondani as a synonym of this, but, as will be pointed out below, we regard this as an error.

Specimens Examined. Numerous examples from sub-species of *O. columbianus* from the following localities in California: Humboldt County; Gualala and Laytonville, Mendocino County. Also from "deer" at Deer Park, British Columbia, Canada, and specimens taken in flight at Sobre Vista and on Mt Wilson and from unstated locality in California.

Notes. The original description of Say contains little of value except the statements that there are "two impressed lines from the base to the margin beyond the middle" of the dorsum of the abdomen and that the venter of the abdomen has an "arquated series of spines near base." These characters will permit the positive separation of the species from *L. subulata* Coq. but not from more closely related forms such as *L. mazamae* Rondani. We present the following notes on the species, indicating the most salient characters.

The sexes are very similar except for the characters associated directly with the genitalia, and we are figuring the female only (Fig. 1).

*Head* above almost destitute of setae. There is some variation, some specimens showing but a single pair of large setae on the front, others showing two pairs and a few smaller setae, but in no case are these setae to be described as numerous. The front (as in most Hippoboscids) shows a median area or frontal vitta which presents a roughened appearance and the posterior margin of which bounds a semicircular area about the ocelli. The form and extent

of these areas appear to afford specific characters. In *L. depressa* the frontal vitta is rather short and broad and the ocellar area correspondingly larger. The ventral side of the head bears a few small setae.

*Thorax* with a row of large but slender pre-alar setae; with an irregular series of smaller setae across the mesonotum; with a group of three post-alars and a group of three or four pre-scutellars on each side; with a median pair of scutellars. On the ventral side both meso- and meta-sterna are thickly beset

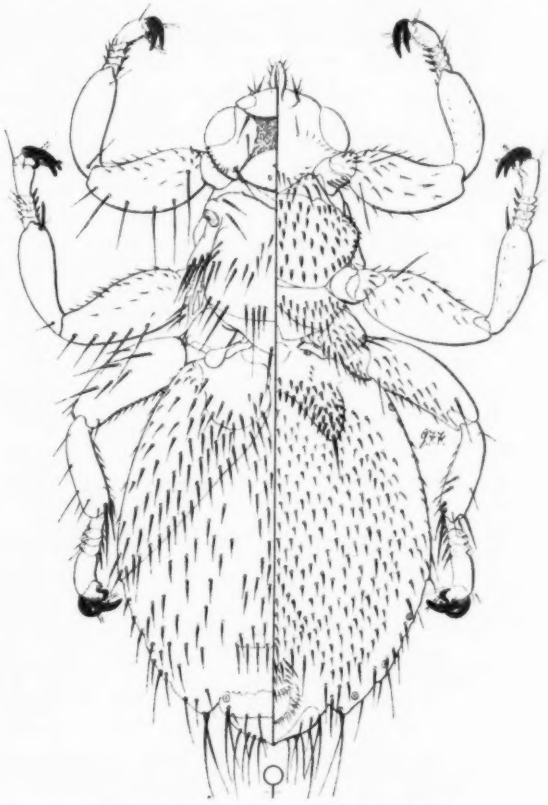

Fig. 1. *Lipoptena depressa* (Say), female.

with short, stout setae. The legs present no special characters except that the anterior tibiae are without an apical seta on the inner margin and that the claws are equal (Fig. 2 *D*).

*Wings* (Fig. 2 *B*) weakly veined as is characteristic of the genus, vein $R_{4+5}$ (the third vein of Dipterists) with a stigma-like expansion at the margin.

*Abdomen* with a conspicuous pair of diverging lines on the dorsum, these lines forming an inverted V and attaining the lateral margins slightly behind

the middle. The spaces between these lines and the lateral margins tend to be more or less chitinized and these areas are beset with numerous setae. Behind these lines the dorsum is membranous except for two small, transverse, pre-apical sclerites, and bears but a few scattered setae.

On the ventral side the basal sternite is quite heavily chitinized and is divided by a deep posterior emargination into two pronounced lobes the tips

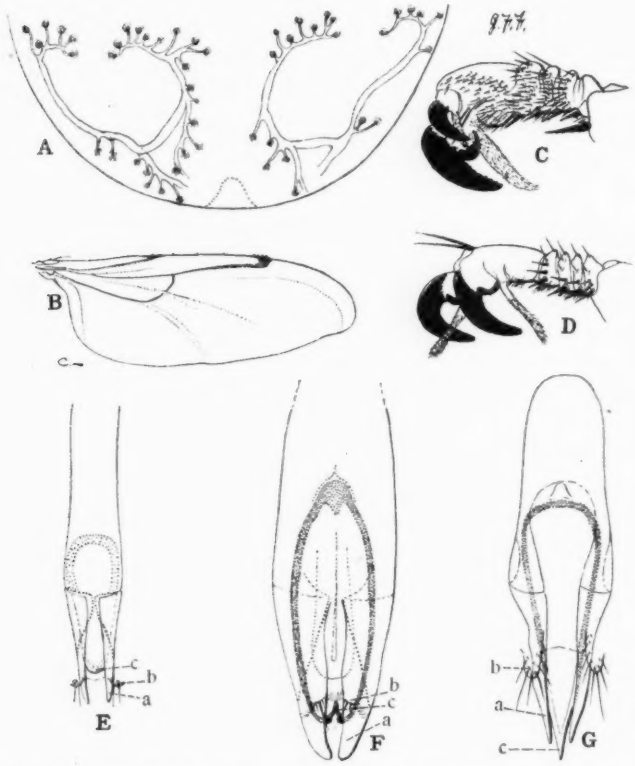


Fig. 2. *Lipoptena mazamae* Rondani: *A*, posterior extremity of larva showing spiracular openings; *E*, genitalia of male. *Lipoptena depressa* (Say): *B*, wing; *D*, anterior tarsus; *F*, genitalia of male. *Lipoptena subulata* Coq.: *C*, anterior tarsus. *Lipoptena traguli* n. sp.: *G*, genitalia of male.

of which are free. The entire sternite is beset with numerous stout setae. The remainder of the venter is quite thickly beset with small, slender setae.

*Genitalia* of the male (Fig. 2 *F*) without external processes, the position of these (*b*) indicated merely by two or three small setae. We are not prepared to discuss the homologies of the internal parts—to do so would necessitate a separate study for which we scarcely have the material—and must content ourselves with a general description. They consist of a pair of stout, chitinized

processes (*a*) attaching basally to a large apodeme or basal plate. Between these two processes is a ring-shaped piece (*c*) which extends forward on to the basal plate and terminates distally in a small point. Within this ring-like piece are some ill-defined structures that probably represent the true penis.

*Lipoptena mazamae* Rondani.

Figs. 2 *A*, 2 *E*.

1878. *Lipoptena mazamae* Rondani, *Ann. Mus. Civ. Genova*, p. 153.
1904. *Lipoptena depressa* (Say), Speiser, *Ibid.* p. 334.
1905. *Lipoptena depressa* (Say), Aldrich, *Catalogue of North American Diptera*, p. 653.

Previous Records. Known only from the original records, from *Cervus mexicanus*, Central America.

Specimens Examined. Three males and two females from skin of a deer, *Mazama* sp., Yacuiba, Bolivia, in the collection of the Field Columbian Museum.

Notes. Speiser (ref. cited) has placed this species as a synonym of *L. depressa*, but if our identification of the species be correct, this is decidedly in error, the genitalia of the males being so different that the two certainly cannot be the same species.

In general appearance *L. mazamae* is very similar to *L. depressa*, so much so, in fact, that the figure given for the female of the latter will apply almost equally well for the former. There are slight differences in the arrangement of the setae, but no more than might be included within the possible range of variation. The presence of a stout apical seta on the inner margin of the anterior tibia will permit the separation of *mazamae*, however. The genitalia of the latter (Fig. 2 *E*) are very different, being not only relatively but actually smaller than in *depressa* and having the inner ring-like piece (*c*) bluntly rounded at the tip.

*Lipoptena traguli* n. sp.

Figs. 2 *G*, 3.

Specimens Examined. Five individuals, the holotype, a female, and one female paratype from *Tragulus subrufus* Lingga Id., China Sea; the allotype and one male paratype from *T. russeus* Tuangku Id.; and one female paratype from *T. rubeus* Pulo Bintang, Rhio Archipelago. All the specimens are from skins in the National Museum and a paratype will be deposited in the collection of that institution.

The hosts are members of the family *Tragulidae*, the "mouse deer."

**Female** (Fig. 3). Length (on slide) 2·75 mm. General colour, pale brown or yellowish.

*Head* with narrow, elongate frontal vitta; the ocellar area much reduced; the front almost destitute of setae, those which may be present rather small; ventral side with but few setae.

*Thorax* dorsally with but few setae; pre-alars slender; two pairs of slender pre-scutellars and two pairs of scutellars, the outer pair of the latter small.

Sternum thickly beset with small, stout setae. Anterior and middle tibiae with a single, stout inner apical seta, the posterior tibiae with two or three such setae; claws of each pair of equal size. Wings and halteres broken off in all the specimens examined.

*Abdomen* with the dorsum marked by two diagonal lines which diverge from the base to the lateral margins well toward the apex, the base of each of the lateral areas thus delimited with a more or less circular, more heavily

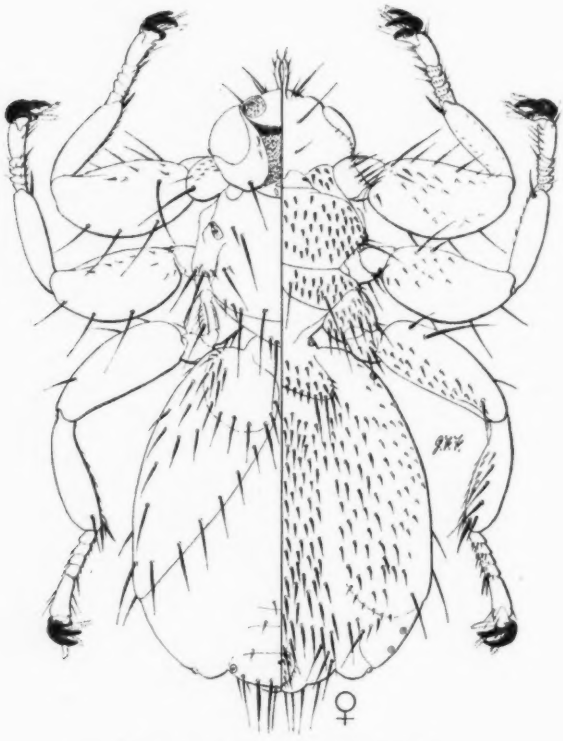


Fig. 3. *Lipoptena traguli* n. sp., female.

chitinized area, the whole sparingly beset with rather large setae. Remainder of the dorsum practically destitute of setae and membranous except for a small pre-apical plate. Basal sternite but slightly emarginate, thickly beset with small, stout setae and with a few longer setae. Remainder of the venter with numerous small, slender setae.

**Male.** Length (on slide) 2·25 mm. In general very closely resembling the female. *Genitalia* (Fig. 2 *G*) with a pair of short external lobes (*b*) which are beset with small setae; internally with the inner ring-like piece (*c*) very sharply pointed at the apex.

NOTES. While in general this species quite closely approaches *L. depressa* it differs in numerous small details including the presence of a stout apical seta on the anterior tarsi and in the character of the genitalia.

*Lipoptena subulata* Coquillet.

Figs. 2 *C*, 4.

1907. *Lipoptena subulata* Coquillet, *Ent. News*, XVIII. 290.

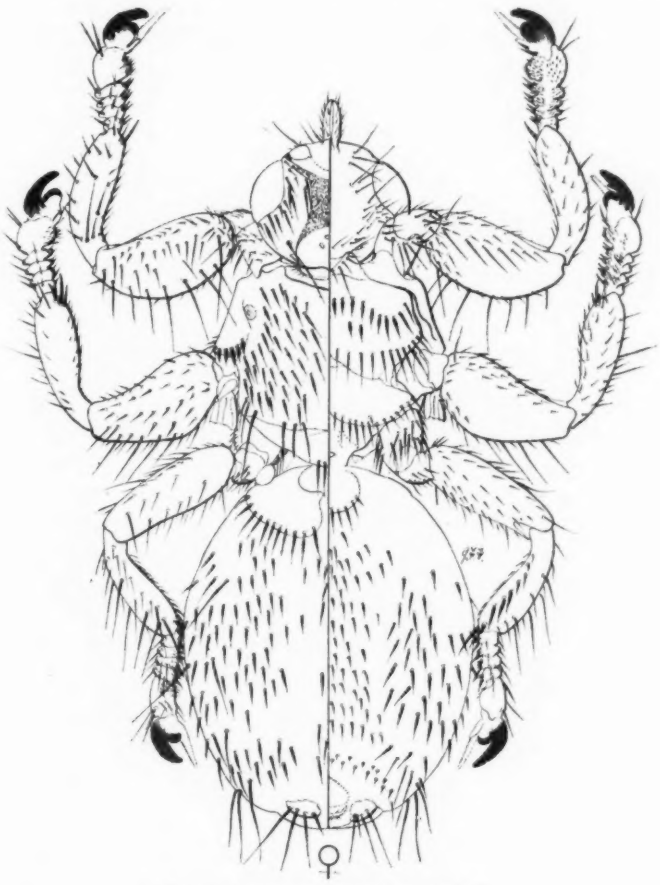

Fig. 4. *Lipoptena subulata* Coq., female.

PREVIOUS RECORDS. From "deer," Woodstock, New Hampshire, U.S.A.

SPECIMENS EXAMINED. Males and females from *Odocoileus columbianus*, Humboldt and Mendocino Counties; from a locality not stated; and specimens taken in flight on Mt Wilson; all from California.

NOTES. The original description contains nothing of value in aiding to identify the species except the statement that there is "a stout black spine at the apex of the inner side of the front tibiae," which is sufficient to distinguish the species from *L. depressa*. We are simply assuming that our specimens represent this species.

The species presents a wealth of structural characters by which it is distinguished from any others that we have examined.

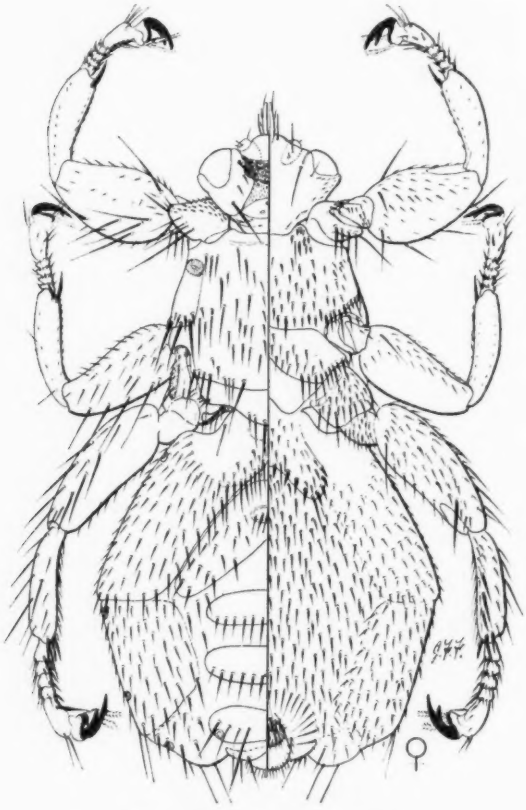

Fig. 5. *Lipoptena cervi* (L.), female.

*Head* beset dorsally with numerous stout setae along the orbits and ventrally with numerous slender setae.

*Thorax* dorsally with a row of short, stout, but sharply pointed pre-alar setae and with numerous small setae on the mesonotum; with a group of three post-alars and three pre-scutellars on each side and with four scutellars.

Ventrally there are two rows of moderately large setae across the mesosternum and a single row across the metasternum. Wings as in *L. depressa*. Legs quite stout; anterior tibiae with a strong, inner apical seta; tarsi (Fig. 2 *C*) with one claw much smaller than the other.

*Abdomen* dorsally without the pair of diverging lines seen in *depressa* but with a pair of basal plates which bear a row of slender setae along the posterior margin. Remainder of the dorsum membranous and with quite numerous setae, except for a pair of small, pre-apical chitinized plates which bear three or four long setae. Basal sternite, rounded posteriorly, not emarginate as in *depressa*, and quite small, bearing a row of small setae. Remainder of the venter with numerous setae, those in the sub-marginal regions larger than the others.

**Male.** In general appearance closely resembling the female. External genitalia merely a pair of small protuberances bearing small setae. The internal genitalia in the two males available are not in condition to figure but appear to resemble those of *L. traguli*.

### *Lipoptena cervi* (Linnaeus).

Fig. 5.

1909. *Lipoptena cervi* L., Massonat, *Ann. de l'Université de Lyon*, N.S. (1), XXVIII. 250–6; Pl. 2, figs. 13–19.

Through the kindness of Major Austen we have received specimens of the female of this species and are figuring it for comparison with the others here described. Massonat (ref. cited) has given a detailed description of the species, accompanied by figures which are quite satisfactory except that the details of the vestiture of setae are not indicated with sufficient clearness. According to this author there is a much greater difference between the sexes than is present in the other species here included.

## Genus **Allobosca** Speiser.

The peculiar species that is the sole representative of this genus is regarded by Speiser as representing also a distinct sub-family.

### *Allobosca crassipes* Speiser.

Figs. 6, 7.

1899. *Allobosca crassipes* Speiser, *Wien Ent. Zeitung*, XXVIII. 199; Fig.

PREVIOUS RECORDS. From *Propithecus diadema* and *Lepilemur mustelinus*, Madagascar. The hosts are lemurs.

SPECIMENS EXAMINED. Five females and one male from skin of *Propithecus edwardsi*, Madagascar, in the United States National Museum.

NOTES. The original description of this species was accompanied only by a figure of the wing and we are taking advantage of the opportunity to

present figures and to add some notes. These are especially desirable as the species is one of considerable interest.

Speiser seems to have been in doubt as to the identity of the sexes, but as he suggested, the female (Fig. 6) has the apex of the abdomen quite deeply

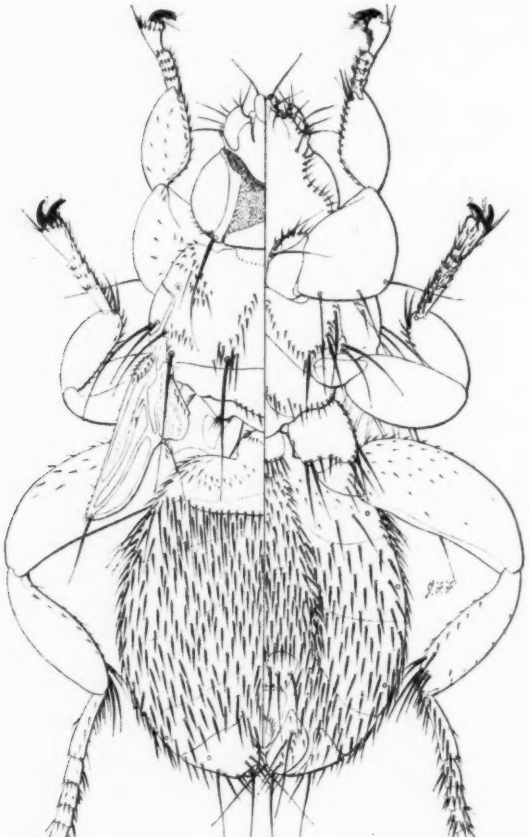

Fig. 6. *Allobosca crassipes* Speiser, female.

bilobed, while in the male (Fig. 7 *B*) it is smoothly rounded. The abdomen of the male bears a large, oval genital plate which is almost destitute of setae. In other respects it is quite as in the female. The genitalia of the male are entirely internal and it has not been possible to make much out of them from the single specimen available.

The clypeal region (Fig. 7 *C*) has the median portion separated by a pair of deep incisions from the lateral parts. The front tarsi (Fig. 7 *D*) differ from the others in the presence of short, almost spatulate setae on the first four segments. The wing (Fig. 7 *A*) was figured by Speiser, but for the sake of completeness we are figuring it again.

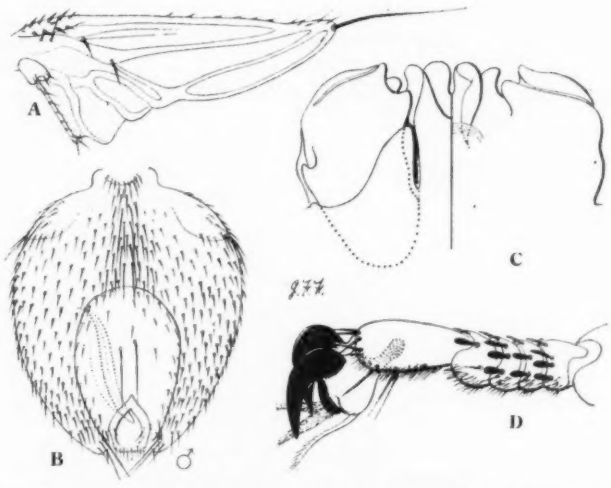


Fig. 7. *Allobosca crassipes* Speiser: *A*, wing; *B*, ventral aspect of abdomen of male; *C*, anterior portion of head; *D*, anterior tarsus.

## Genus **Melophagus** Linnaeus.

An apology may be deemed advisable for discussing this well-known genus but our attention has been attracted to it by the discovery of an apparently new form, and in connection with the description of this some general notes may not be out of place. Furthermore, as far as we have been able to determine, there exists no illustration of any species of the genus that is of any particular value from a systematic standpoint. The crude figures that adorn the pages of most of our textbooks of parasitology, at least, can scarcely be regarded as pre-occupying the field, for at the best they show little more than the general characters of the genus.

Massonat (1909) has discussed at some length the question of the homology of the small projection at each posterior angle of the thorax which some authors seem to have regarded as a haltere. He arrives at the conclusion that these structures are in reality vestigial wings and with this conclusion we are entirely in accord. In fact their position is such that they cannot be halteres unless a most remarkable shifting of the position of these organs has taken place. They are to be regarded as almost the irreducible minimum of wing vestiges. No trace of the halteres can be found.

*Melophagus ovinus ovinus* Linnaeus.

Figs. 8, 9 *A–D*.

PREVIOUS RECORDS. A cosmopolitan species on domestic sheep. Speiser has described a "variety," *M. ovinus ferus*, from "Steinbok" in the Caucasus.

SPECIMENS EXAMINED. From domestic sheep in various parts of the United States.

NOTES. The accompanying figures will form a basis for the comparison of this species with other closely related forms such as that which we are describing below. The differences will be pointed out in connection with the description of this form.

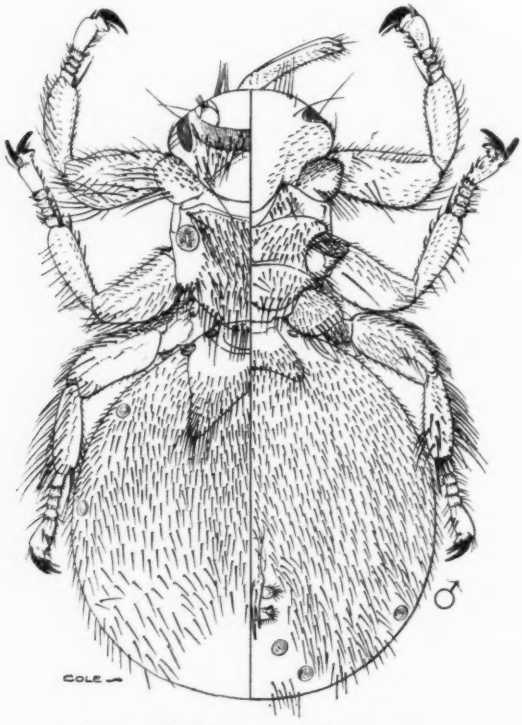


Fig. 8. *Melophagus ovinus ovinus* L., male.

*Melophagus ovinus montanus* new sub-species.

Figs. 9 *E*, 10.

SPECIMENS EXAMINED. Males only, from "mountain sheep," probably either *Ovis dalli* or *O. canadensis*, on the Alaska-Yukon boundary. The specimens, which have been in the Stanford Collection for some years, were received from the late Dr C. Gordon Hewitt.

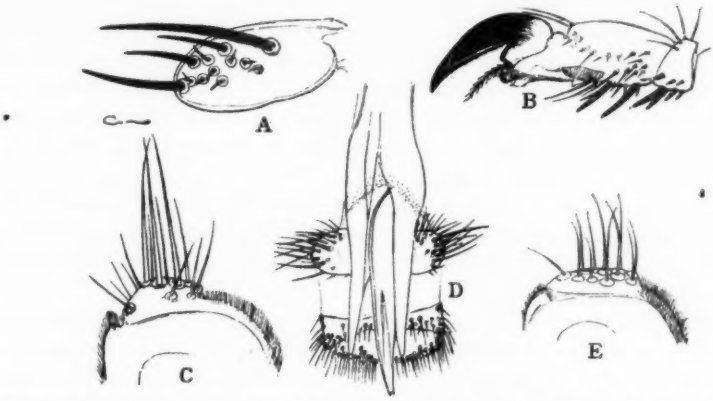


Fig. 9. *Melophagus ovinus ovinus* L.: *A*, wing vestige; *B*, portion of anterior tarsus; *C*, tip of antenna; *D*, genitalia of male. *Melophagus ovinus montanus* n. ssp.: *E*, tip of antenna.

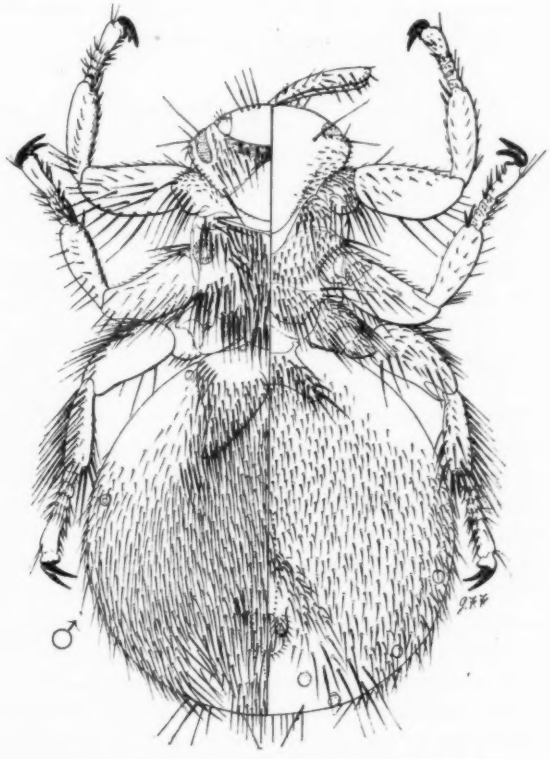

Fig. 10. *Melophagus ovinus montanus* n. ssp , male.

**Male** (Fig. 10). Differing from the male of *M. ovinus ovinus* (Fig. 8) in the following particulars especially. Setae everywhere tending to be larger and more numerous, the difference in size being especially conspicuous on the dorsum of the thorax; abdomen above without a bare apical space as in the male of *ovinus ovinus*; scutellum apparently lacking and no scutellar setae present, while in the typical form the scutellum, although very small, is distinct and bears a cluster of apical setae.

There appears to be a slight difference in the antennae, the typical form (Fig. 9 *C*) having the apical setae much longer than they are in *montanus* (Fig. 9 *E*). The wing vestiges, genitalia and claws seem to be the same as in the typical form (Fig. 9 *A*, *B*, *D*).

Notes. While these two forms are certainly closely related we cannot but regard them as worthy of distinction. The differences are small, but upon a direct comparison of specimens are sufficiently evident. A sufficient amount of material of the typical form has been examined without evidence of variation to reduce the chance that *montanus* is simply a variant.

A comparison with *M. ovinus fera* Speiser is not possible, for the description of this form consists merely of the statement that "sie ist etwas schlanker, etwas heller und etwas kleiner" than the typical form.

### Genus **Olfersia** Wiedemann.

### *Olfersia americana* (Leach).

Figs. 11, 12.

1905. *Olfersia americana* (Leach), Aldrich, *Catalogue of North American Diptera*, p. 655.

Previous Records. A widely distributed and often recorded species, infesting chiefly owls, in North America. Massonat (1909) has recorded the species from *Platalea leucorodia* in France, but, if we may rely upon his figures, his specimens represent an entirely distinct species.

Specimens Examined. Numerous examples from California and from Washington, District Columbia, from various species of owls.

Major Austen has very kindly compared one of our specimens with the type of this species in the British Museum and has confirmed this determination.

Notes. The accompanying figure of the female (Fig. 11) should make the recognition of this species relatively easy. It is usually a reddish-brown species, some specimens being paler than others. The antennae are comparatively small and are strongly bristled at the apex. The frontalia is quite large and the orbits are wide. The section of horizontally striated membrane down the centre of the dorsum of the abdomen is quite noticeable. The chaetotaxy and form of the male are essentially the same as in the female. The male genitalia are characteristic, consisting mainly of two slender, pointed side pieces, possibly corresponding to the superior forceps, and a long central piece which is curved at the base, rather heavily chitinized and pointed. This may be

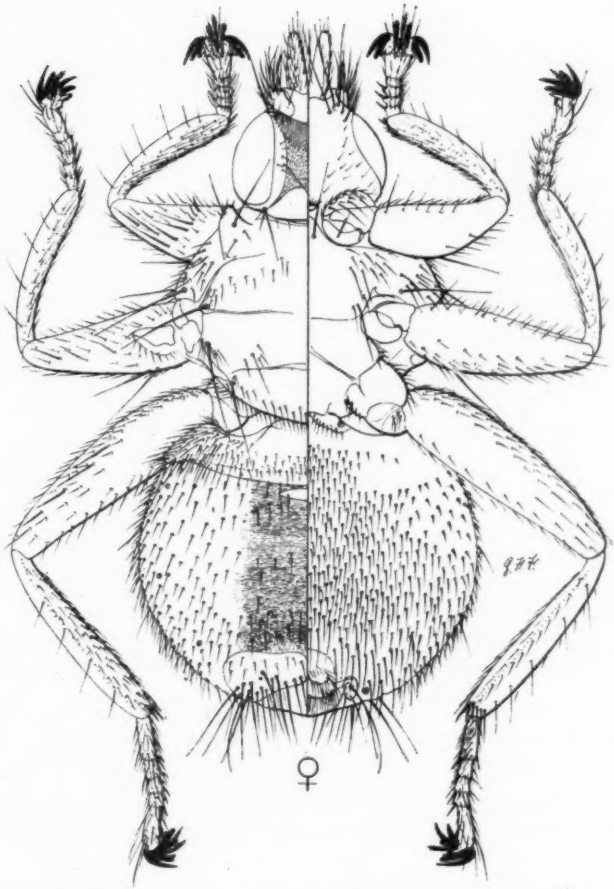

Fig. 11. *Olfersia americana* (Leach), female, from "barn owl," *Aluco pratincola*, San Bernardino, California.

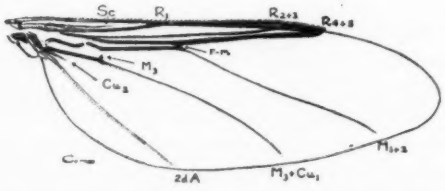


Fig. 12. *Olfersia americana* (Leach), wing. Lettering of venation according to Comstock-Needham system.

the aedeagus as there is a chitinized piece at the base, evidently the apodeme of the penis.

The hind tibiae suggest those of *Pseudolfersia spinifera*, described below, but the small tubercles are in a single row and the circular structures near them are slightly different in appearance. The posterior tarsi are toothed on the margins, but not so strongly as in *P. spinifera* and the teeth do not extend to the apex of the last segment. The outer tooth of the claws is very slender, the middle tooth distinctly wider and with a blunt, rounded tip. The arrangement of the fine setulae on the wing membranes is like that figured for *P. spinifera*, but there are not so many in the basal part of the wing and none at all in the anal region.

Our interpretation of the wing venation (Fig. 12) is in accord with the Comstock-Needham system of nomenclature. Massonat (1909) who has attempted to apply this system seems not entirely to have understood it and has arrived at results which are impossible under its application. His $R_3$ is in reality $R_{4+5}$, his $R_2$ is $R_{2+3}$.

## Genus **Pseudolfersia** Coquillet.

### *Pseudolfersia spinifera* (Leach).

Figs. 13, 14.

1818. *Feronia spinifera* Leach, *Mem. Wernerian Nat. Hist. Soc.* II. 557; Pl. 26, figs. 1–3.
1901. *Pseudolfersia diomedeae* Coquillet, *Proc. Washington Acad. Sci.* III. 379.
1902. *Pseudolfersia spinifera* (Leach), Speiser, *Zeitschr. f. syst. Hym. und Dipt.* II. 146–149.
1903. *Olfersia vulturis* Van der Wulp, *Biologia Centrali Americana, Diptera*, II. 429; Pl. 13, figs. 1–1 *a*.
1903. *Pseudolfersia vulturis* (Van der Wulp), Austen, *Ann. Mag. Nat. Hist.* (7), XII. 261.
1903. *Pseudolfersia spinifera* (Leach), Austen, *Ibid.* p. 265.

Previous Records. A tropicopolitan species occurring on a wide range of hosts including especially sea birds. Austen (ref. cited) gives a list of the species from which it has been taken and also a list of the names that have been applied to it.

Specimens Examined. A paratype male of *Pseudolfersia diomedeae* Coq., from *Diomedea irrorata*, Galapagos Ids.; a single male from *Fregata aquila*, Cape San Lucas, Lower California; three males from "king vulture," Belize, British Honduras. All of these specimens from the Stanford University collection.

Notes. We are entirely convinced that the specimens that we have examined represent but a single species—*P. spinifera* (Leach). Major Austen has kindly compared one of our specimens from "king vulture" with the type of *vulturis* in the British Museum and has identified it as this species. Our specimen from frigate bird agrees exactly with the very good description of *spinifera* given by Speiser and as this species is known to occur characteristically on the frigate bird, we do not doubt the correctness of our determination. The distribution of the species is remarkable, but it should be borne in mind

that certain of its hosts are wide ranging forms, both as species and as individuals.

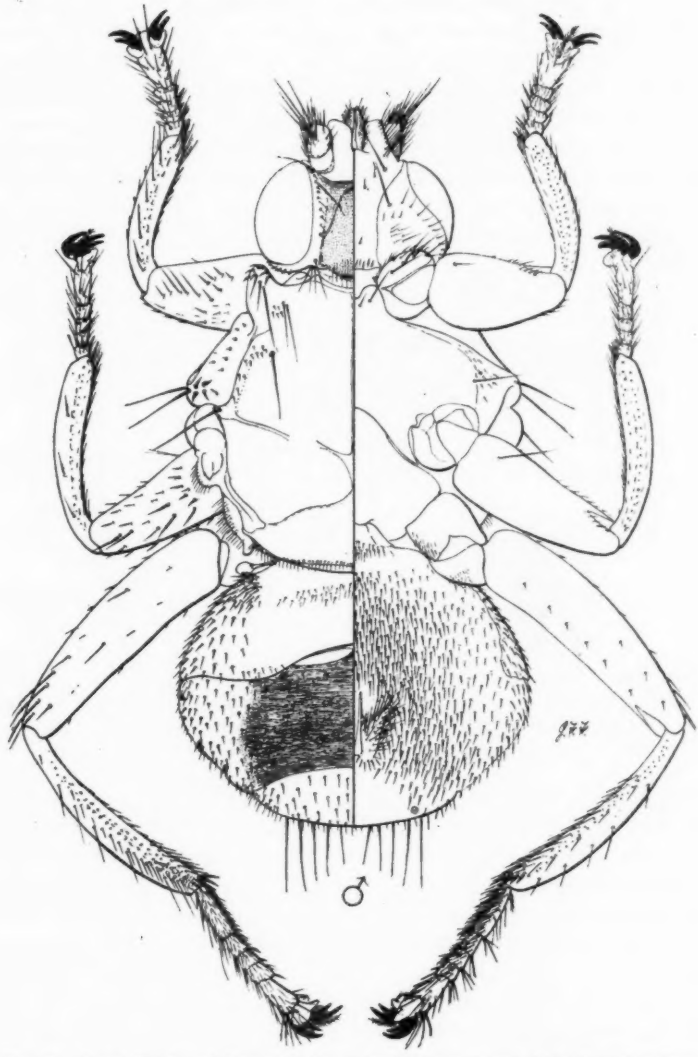

Fig. 13. *Pseudolfersia spinifera* (Leach), male. From paratype of *P. diomedeae* Coq.

We present the following notes on the morphology of the species.

*Head* with no strong fronto-orbital bristles.

*Thorax* with the mesonotum almost bare, the scutellum with a marginal row of very small setae. Sternum practically entirely bare. The tibiae and

tarsi show what are probably good specific characters in the arrangement of the setae and in the presence of small, tooth-like projections on the tarsi. The hind tarsi (Fig. 14 *B*) have a row of these teeth along each ventral margin of each segment; on the front tarsi there are but two of these teeth near the base of the last segment. The hind tibiae have, in addition to setae and small spines, a large number of small circular structures near their apices (Fig. 14 *C*) which are probably sensory pits.

*Wings* (Fig. 14 *A*) with the whole membrane, back to the basal cross veins, densely beset with microscopic setulae which cannot be shown in the figure; the stippled portion in the figure is so densely beset with these setulae as to appear gray, the remaining portion is yellowish and has only a thin covering of setulae.

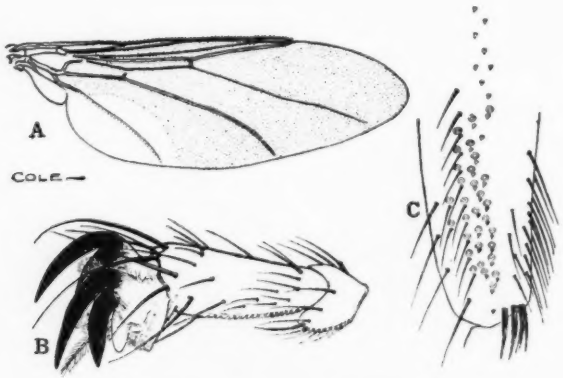


Fig. 14. *Pseudolfersia spinifera* (Leach): *A*, wing; *B*, portion of posterior tarsus; *C*, apex of posterior tibia. From paratype of *P. diomedeae* Coq.

*Abdomen* with the basal, chitinized portion of the dorsum extensive. The median portion of the dorsum bears a broad area of fine, dense striations and the posterior fourth of the dorsum is chitinized. The ventral side is thickly beset with fine setae.

The genitalia of the male show a pair of quite long, tapering external processes and internally a pair of pointed structures, probably the superior forceps.

The specimens from "king vulture" differ very slightly from the others, having the anal area of the wing entirely bare of setulae and the cell 2*M* (second basal) noticeably wider and shorter. However, the latter character is somewhat variable in the specimens examined.

Genus **Ornithomyia** Latreille.

*Ornithomyia avicularia* (Linnaeus).

Figs. 15, 16.

1909. *Ornithomyia avicularia* (L.), Massonat, *Ann. de l'Université de Lyon*, N.S. (1), XXVIII. 271–78; Pl. 4, figs. 33–34.

1921. *Ornithomyia anchineuria* Speiser, Cole, *Proc. Calif. Acad. Sci.* (4), XI. 344.

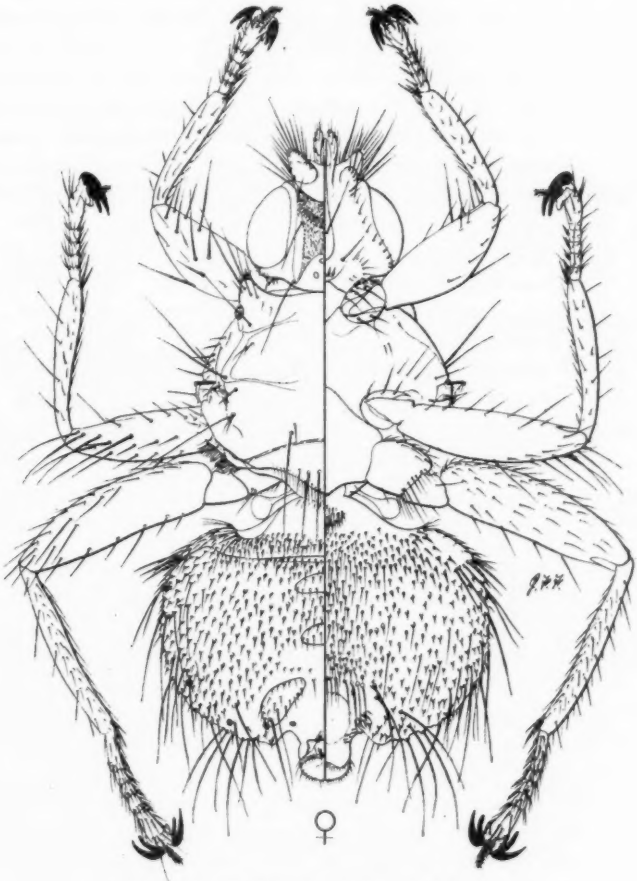

Fig. 15. *Ornithomyia avicularia* (L.), female.

PREVIOUS RECORDS. A widely distributed European and North American species on many passerine and raptorial birds.

SPECIMENS EXAMINED. Two females, one from Keyport, Washington, without indication of host, and one from *Sayornis sayi*, Pacific Grove, California,

both in the Stanford University collection; one male from *Cyanocitta stelleri*, Upper Alsea River Valley, Oregon, in the collection of the junior author. This last specimen has previously been recorded by Cole (ref. cited) as *O. anchineuria* Speiser.

NOTES. There have been numerous descriptions of this species but only that given by Massonat (ref. cited) is sufficiently precise and accompanied by such figures as to make identification definitely possible. Our specimens agree very closely with the figures given by this author, but as there are certain chaetotactic details which he has not included we are figuring it again.

Some of the chaetotactic characters are possibly generic and some are undoubtedly specific. There appears to be some slight variation in the size and arrangement of the bristles. The abdomen is densely beset with small setae (Fig. 15) and bears numerous large setae, the position of which is apparently constant. In addition to the basal plate there are on the dorsum

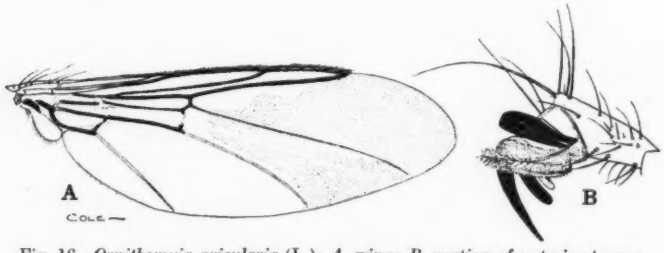


Fig. 16. *Ornithomyia avicularia* (L.): *A*, wing; *B*, portion of anterior tarsus.

three small median plates (the anterior-most of which is partially concealed beneath the basal plate in the figure) and a pair of larger plates near the apex.

The figure of the abdomen of the female given by Massonat indicates that the apex of the abdomen is quite deeply bilobed, while in our specimens there is a median lobe. This lobe, however, is membranous and is probably more or less retractile, and we are not inclined to regard this difference as important. The abdomen of the male differs from that of the female chiefly in not being lobed at the apex and in having a complete, transverse, pre-apical plate instead of the paired plates of the female. The genitalia show no external processes; the internal structures consist of a pair of slender, pointed, lateral processes and a pointed median process.

The wing venation is characteristic, $R_1$ (first vein) ending considerably before the radio-medial (first) cross-vein. The fine setulae are confined to a definite area as indicated in the figure. The costa is covered with short, bristly setae, especially dense beyond the end of $R_1$.

Genus **Stilbometopa** Coquillet.

*Stilbometopa impressa* (Bigot).

Figs. 17, 18.

1885. *Olfersia impressa* Bigot, *Ann. Soc. Ent. France*, p. 257.
1902. *Stilbometopa impressa* (Bigot), Speiser, *Zeitschr. f. syst. Hym. und Dipt.* II. 163.

Previous Records. Originally recorded by Bigot from California and recorded by Speiser from a specimen from California.

Specimens Examined. A female taken from "valley quail," *Lophortyx californica*, California, in the collection of the California Academy of Sciences; one female from Mecca, California, without indication of host, in the same collection; one broken specimen of undeterminable sex from "quail," Mount Hamilton, California, in the Stanford University collection; one female, without indication of host, from San Diego, California, June, 1921.

Notes. Speiser (ref. cited) gives a very good re-description of this species from the type. It is an easily recognizable form of very peculiar character. It is interesting to note that the type of the genus which is the only other included species, *S. fulvifrons* (Walker), also infests gallinaceous birds, Austen having reported it from *Ortyx virginiana*, *Geotrygon sylvatica* and *G. montana*, among other hosts.

The colour of the body is evidently to some extent variable, some specimens being yellowish brown, others blackish. The setae on the legs and antennae are blackish, those on the frons and mesonotum yellowish. The face, clypeus and underside of the head are yellowish. There are few setae on the mesonotum and these are placed in definite areas as indicated (Fig. 17).

The antennae in Fig. 17 are pointing downward, their shape is better shown in Fig. 18 *B*.

The prothoracic spiracles are very large and heavily chitinized. The scutellum has a distinctive shape, being very broad and almost emarginate posteriorly. On each side of the thorax, just under the vestigial squamae, is a remarkable, heavily chitinized, hammer-shaped projection, that is very distinctive of the species.

The abdomen has a dense covering of short setae borne upon small tubercles, most of these setae being short and heavy. The basal, chitinized portion of the dorsum is large and the remainder is membranous except for a pair of plates near the apex. The ventral side is entirely membranous except for a pair of plates on the anterior margin of the vulva.

The ungues (Fig. 18 *C*) have the outer tooth much longer than the second; the few setae on the last tarsal segment are strong, a blunt seta near the base of the pulvilli being especially noticeable.

The wings (Fig. 18 *A*) are entirely destitute of the microscopic setulae that are present in all the other bird-infesting forms known to us. The veins near the base and anterior margin of the wing are heavy and black and there is a thick anal cross-vein ($Cu_2$).

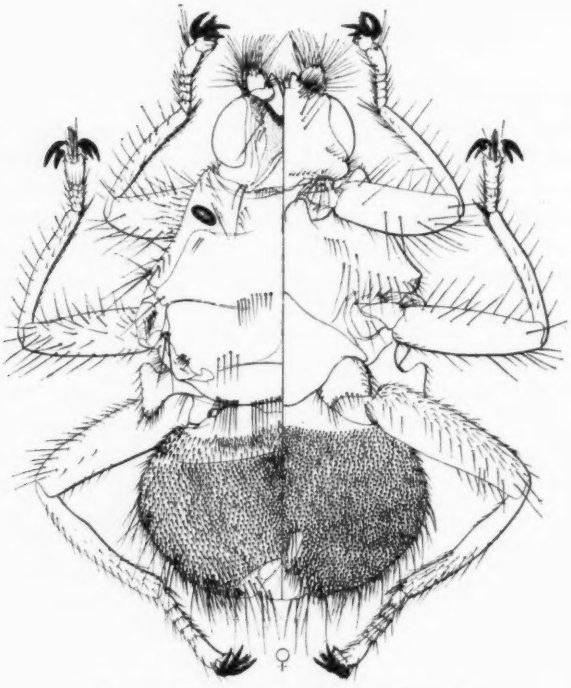

Fig. 17. *Stilbometopa impressa* (Bigot), female.

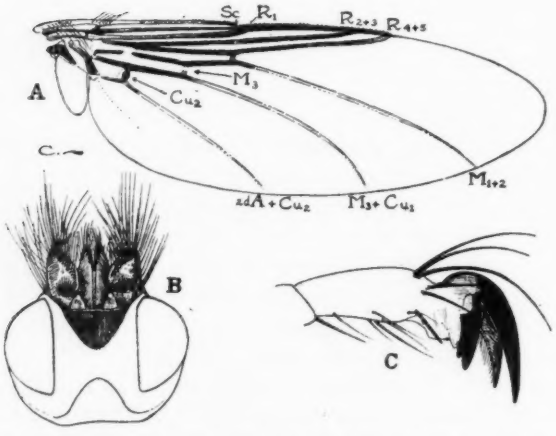


Fig. 18. *Stilbometopa impressa* (Bigot): *A*, wing, lettering in accordance with the Comstock-Needham system; *B*, head; *C*, portion of tarsus.

Genus **Ornithoica** Rondani.

*Ornithoica promiscua* n. sp.

Figs. 19, 20.

. SPECIMENS EXAMINED. Holotype, a female, in the collection of the California Academy of Sciences, taken from *Pipilo crissalis carolae*, Castle

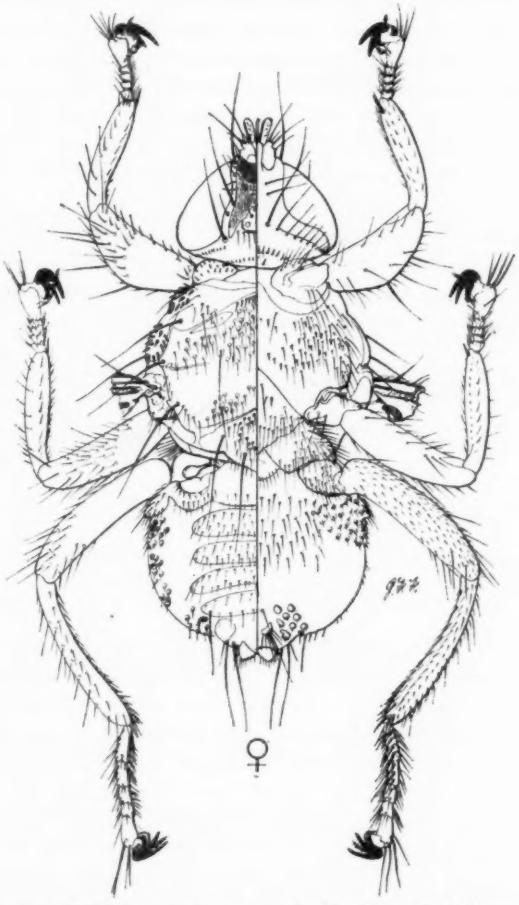

Fig. 19. *Ornithoica promiscua* n. sp., female. From the holotype.

Hot Springs, Lake County, California, Sept. 23, 1920 (J. Maillard). Three female paratypes all from California; one from "fox sparrow," San Francisco, Dec. 5, 1919 (L. Little), in the same collection; one from *Regulus calendula*, Pacific Grove, Jan. 25, 1904; one from *Falco sparverius*, King's River; the last two in the Stanford University collection.

**Female** (Fig. 19). Length (on slide) 2·5 mm. A yellowish brown species, the thorax darker than the legs.

*Head* with the frons probably almost parallel-sided in perfect specimens but in the holotype curving in slightly. Frontal orbits with at least three strong setae and several smaller setae. Ocellar setae small. Ventral side with a row of slender setae more or less paralleling the orbits.

*Thorax* with several short, stout, black setae on the humeral callosities and on the margin in front of the wing. Mesonotum with numerous small, pale setae, all with distinct pustulations about the base. There is a single long seta just behind the humeral callosity, two in front of the wing and one just behind the wing. Scutellum with small, pale, pustulated setae on the disc and with four long, black setae. Halteres rather small and delicate.

On the ventral side both meso- and meta-sternum are beset with numerous fine setae, mingled with a few that are small and stout.

*Wings* (Fig. 20 *A*) with a well-defined anal cell; $R_{2+3}$ distinctly curved toward the costa and bristly to the tip; *m-cu* cross-vein broken, the upper part obsolete; vein above cell 2*M*, broken near the middle; distal half of the wing covered with microscopic setulae as shown in the figure.

Fig. 20. *Ornithoica promiscua* n. sp.: *A*, wing; *B*, anterior tarsus.

*Legs* comparatively strong, the anterior femora noticeably thickened; setae arranged in a rather definite fashion, as shown in the figure. Claws (Fig. 20 *B*) rather slender.

*Abdomen* above with a chitinized basal plate extending from side to side, with four quite large plates occupying the median half and with a small plate on each side of the anal region, the basal plate and the succeeding four with numerous small setae and the para-anal plates or their immediate region with two long setae. Lateral margins with a number of small, stout setae which are borne on tubercles. On the ventral side there is a median region beset with small setae, a region along the anterior, lateral margin with numerous setae on tubercles and a smaller region of these near the genital opening. Near the genital opening there is also a pair of small plates bearing several slender setae.

Notes. One other species of this genus, *O. confluens* (Say), has been recorded from North America, and, as far as we can learn, all references to this species have been based upon Say's description. We regard *confluens* as unrecognizable from this description and are therefore describing our species as new. *O. confluens* was taken from *Ardea candidissima*.

Austen (1903) states that *O. vicina* (Walker) may be a synonym of *confluens*, that *O. beccariina* Rondani from Amboina, on *Ardea alba*, is identical with

*O. exilis* (Walker) from New Guinea, and that this too is probably the same as *vicina*.

Our species is certainly very close to *O. turdi* (Latreille) (Massonat, 1909) from Europe. Certain differences are evident on the basis of Massonat's description and figures, but it is not at all improbable that these differences might disappear upon a comparison of specimens.

Two specimens from "California russet-backed thrush," *Hylocichla ustulata*, without indication of locality, differ somewhat from the typical *promiscua*, the setae being in general fewer and smaller, approaching more closely *turdi*, but our material is not in the best of condition, and for the present we place them provisionally with *promiscua*.

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AUSTEN, E. E. (1903). Notes on *Hippoboscidae* (Diptera Pupipara) in the Collection of the British Museum. *Ann. Mag. Nat. Hist.* (7), XII. 255–266.

MASSONAT, E. (1909). Contribution a l'Étude des Pupipares. *Ann. de l'Université de Lyon*, N.S. (1), XXVIII. 1–356; Pls. 1–7.

# THE STRUCTURE AND SYSTEMATIC POSITION OF *STRONGYLUS POLYGYRUS*.

By C. L. BOULENGER, M.A., D.Sc.

(*From the Zoological Department, University of Birmingham.*)

(With 4 Text-figures.)

Dujardin (1845) was the first to give a satisfactory account of the small Strongylid worms inhabiting the intestinal tract of field-mice and voles. His descriptions of the various species were careful and for the most part accurate, they were, unfortunately, not accompanied by figures, and incomplete in that the characters of the bursal rays of the males were not given, an omission which has led to considerable confusion, since the modern classification of the Trichostrongylidae is based largely on the structure of the male bursa.

Of the four worms described by Dujardin, *Strongylus costellatus* has been taken as the type of the genus *Heligmosomum* Railliet and Henry (1909), to which genus his other species *S. minutus*, *S. laevis* and *S. polygyrus* were also assigned. On the authority of Travassos (1914) *S. polygyrus* has since been removed to his genus *Viannaia* by Hall (1916) who, however, remarks that the available descriptions are not sufficiently detailed to warrant the change.

I have recently been fortunate in obtaining a number of small Strongylids from the intestine of *Microtus* (*Arvicola*) *agrestis* L. from the neighbourhood of Birmingham, which I am convinced belong to the same species as that described by Dujardin as *S. polygyrus*, their study has enabled me to clear up a number of misconceptions with regard to this form.

Von Linstow (1878, 1879 and 1882) is the only authority since Dujardin who has attempted to reinvestigate the species; his account contains descriptions and figures of the male bursa, but in certain important characters the worm studied by him seems to deviate so much from the original specific diagnosis that Hall (1916) felt justified in concluding that a different form had been dealt with by the German helminthologist, and in removing it to a new genus *Heligmosomoides* under the designation *H. linstowi* Hall. Travassos (1921) accepts Hall's conclusions and in his recent monograph on the Trichostrongylidae we find *S. polygyrus* Dujardin listed as *Viannaia polygyra* and *S. polygyrus* von Linstow as *Heligmosomoides linstowi*.

My investigations of the new material have led me to a quite opposite conclusion, and I am convinced that Dujardin and von Linstow have dealt with the same species. The specimens before me agree in all important characters with *S. polygyrus* as described by the French author; at the same time it is quite easy to reconcile my account of the male bursa with von Linstow's description and figures. The confusion has been due largely to the latter's mistake with regard to the position of the vulva of the female, but partly also to a misunderstanding of Dujardin's original description by some recent authors.

Dujardin's specific diagnosis of *S. polygyrus* clearly shows that one of the important characters of the species is the shape of the female tail, the latter being narrow, conical, truncated posteriorly and terminated by a slender, transparent spike 0·02 mm. in length; the anus is given as 0·075 mm. from the posterior extremity. The shape of the tail is therefore very similar to that found in species of the genus *Nematodirus*.

Hall (1916) has evidently misunderstood Dujardin's account, in his diagnosis he gives "Tail 20$\mu$ long, thin, conical, diaphanous, truncated, and terminating abruptly in a narrow point. Anus 75$\mu$ from the tip of the tail," further commenting on the fact that Dujardin evidently does not regard the length of the tail and the distance from the anus to the tip of the tail as the same thing. Dujardin's actual words are "queue amincie, conique, tronquée, et terminée brusquement par une pointe grêle, diaphane, longue de 0 mm., 02; —anus à 0 mm., 075 de l'extrémité." The measurement 0·02 mm. here clearly refers to the length of the terminal spike, not to that of the tail.

It is evident therefore that in the shape of the female tail, with its truncate extremity and terminal spike, we have an important character which distinguishes *S. polygyrus* from *S. costellatus*, the type species of the genus *Heligmosomum*. The form examined by von Linstow clearly possessed this character, the anus being described as 0·098 mm. from the end of the tail and definite reference made to a slender, terminal spike, 0·016 mm. long.

Von Linstow described the vulva as 0·24 mm. from the head end, one of the chief characters used by Hall and Travassos in separating *S. polygyrus* v. Linst. from *S. polygyrus* Duj.; this statement I think, however, should be regarded as a clerical error, *Kopfende* having been accidentally substituted for *Schwanzende*. The distance 0·24 mm. from the head end would place the vulva anterior to the termination of the oesophagus, an almost impossible situation in this group of Nematodes; von Linstow's description of the ovejector (1882) is, moreover, incompatible with such a forward position for the vulva.

The specimens obtained by me from the Birmingham voles agree with those described by Dujardin and von Linstow in so far as the shape of the tail and the position of the anus are concerned. The vulva was found to be situated 0·24–0·35 mm. from the *posterior* extremity.

Dujardin's account contains little useful information with regard to the

male organs, the spicules are, however, given as 0·58 mm. long, this measurement agreeing well with von Linstow's (0·54 mm.) and that observed by me in the new material (0·5–0·58 mm.).

Von Linstow's description and figures of the male bursa have given rise to much discussion; according to his account the bursa of *S. polygyrus* has no separate dorsal lobe and no median dorsal ray, the latter being replaced by two rays with separate origins; between these and behind the cloaca are shown seven pairs of small ray-like structures ending in papillae. The bursal characters as figured by von Linstow differ so much from those of other species now assigned to the genera *Heligmosomum* and *Viannaia* as to justify Hall's transference of the worm to a new genus *Heligmosomoides*.

Travassos (1921) accepts the systematic position assigned to the species by Hall, but adopts a somewhat different interpretation of von Linstow's figures of the bursa; he prefers to regard the two dorsal rays as representing the externo-dorsal rays of other species, and the true dorsal rays as being replaced by the seven pairs of small post-cloacal rays.

My material has shown that Travassos' interpretation is the more correct. In the Birmingham specimens the male bursae bear a striking resemblance, both in shape and in the general arrangement of the ventral and lateral rays, to those figured by von Linstow. When completely spread out and viewed from the dorsal or ventral aspect (text-fig. 3) the bursa is seen to be of considerable width with an almost straight dorsal margin, without a separate dorsal lobe or marked median incision. There are two long, slender externo-dorsal rays with separate origins, and, between them, a very small median dorsal ray branching dichotomously into four delicate branches. A genital cone is well developed, bearing one or two pairs of small, but highly refractile papillae on each side of the cloaca.

In an incompletely extended bursa, as shown in text-fig. 4, the two externo-dorsal rays appear much closer together and the genital cone covers and hides the greater part of the dorsal ray, revealing only the tips of the four branches which, together with the cloacal papillae, give the appearance of a series of small rays in the neighbourhood of the genital opening.

The peculiarities of von Linstow's figures of the bursa of *S. polygyrus* are thus readily explained; comparison of these figures (1878, Fig. 21 and 1879, Fig. 26) with my own (text-figs. 3, 4) will show conclusively that the form described here is specifically identical with that studied by the German authority.

The facts stated above make it clear that there is no justification for the separation of *S. polygyrus* Duj. and *S. polygyrus* v. Linst. It is evident from the structure of the female tail and from the peculiarities of the male bursa that the species cannot be referred to either of the genera *Viannaia* or *Heligmosomum*; Hall's genus *Heligmosomoides* must therefore be retained, the worm, however, figuring as *H. polygyrus* (Duj.) instead of *H. linstowi* Hall.

A revised diagnosis of the genus *Heligmosomoides* is given below, together with a new specific diagnosis of *H. polygyrus* based on the material before me:

## HELIGMOSOMOIDES Hall, 1916.

*Generic diagnosis.* Heligmosominae: Body commonly coiled in a spiral, with transverse and longitudinal striations. Male with long, filiform spicules. Bursa without separate dorsal lobe or middorsal incision. Dorsal ray very short with four small branches. The externo-dorsal rays are long and slender, with separate origins. The lateral rays arise from a common trunk and are divergent. Ventro-ventral and latero-ventral rays divergent with a common origin. Prebursal papillae long. Female with a truncated posterior extremity bearing a slender caudal spike. Vulva situated posteriorly.

Type species. *H. polygyrus* (Dujardin, 1845).

### **Heligmosomoides polygyrus** (Dujardin, 1845).

Synonyms: *Strongylus polygyrus* Dujardin, 1845.
„ „ von Linstow, 1878.
*Heligmosomum polygyrum* Railliet and Henry, 1909.
*Viannaia polygyra* Hall, 1916.
*Heligmosomoides linstowi* Hall, 1916.

Small worms, reddish in colour when alive, and usually coiled in a spiral.

The head, 0·04–0·05 mm. wide, is provided with a cuticular expansion, usually asymetrically developed and with conspicuous transverse striations (text-fig. 2). Head papillae appear to be present, but their number and arrangement could not be definitely ascertained.

The cuticle of the body is striated both longitudinally and transversely, there are, moreover, 18–20 longitudinal crests. The transverse striations are very fine and most apparent along these crests and in the neighbourhood of the vulva of the female.

The oesophagus is short, 0·48–0·6 mm. in length. There is a small buccal cavity with chitinous walls.

**Male:** 4·5–5·5 mm. long, with a maximum thickness of 0·07–0·09 mm. in the posterior part of the body.

The bursa has a length of 0·17–0·18 mm. and a breadth of 0·3–0·33 mm. The dorsal edge of the bursa is almost straight (text-fig. 3), there is no separate dorsal lobe or median dorsal incision separating the lateral lobes.

The dorsal ray is slender and very short, branching dichotomously into four small rays, the total length of dorsal ray and its branches measures 0·025–0·035 mm. In the neighbourhood of the dorsal ray the bursa is frequently transversely folded, so as to give the appearance of an accessory bursal membrane. The externo-dorsal rays are long and slender, they have

separate origins and extend almost to the margin of the bursa. The lateral rays arise from a common trunk and are divergent; the postero-lateral ray is

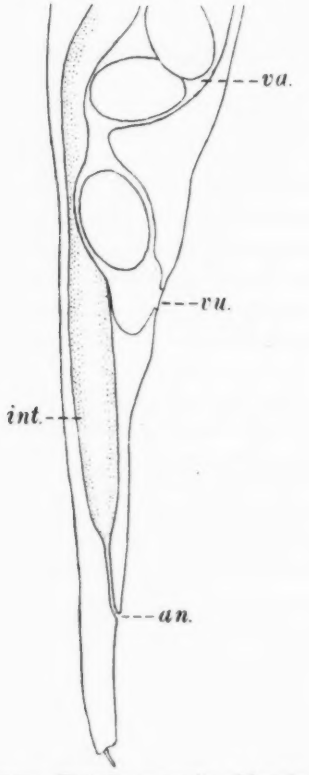


Fig. 1. *Heligmosomoides polygyrus.* Posterior extremity of female, lateral view. × about 220.

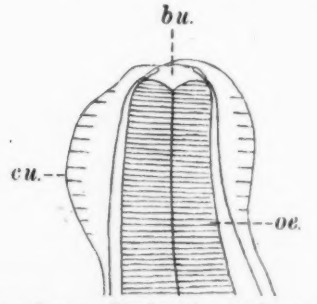


Fig. 2. *Heligmosomoides polygyrus.* Head, with cuticular expansion. × about 650.

only slightly thicker than the externo-dorsal and runs almost parallel with it, the medio-lateral and externo-lateral rays are considerably thicker than the

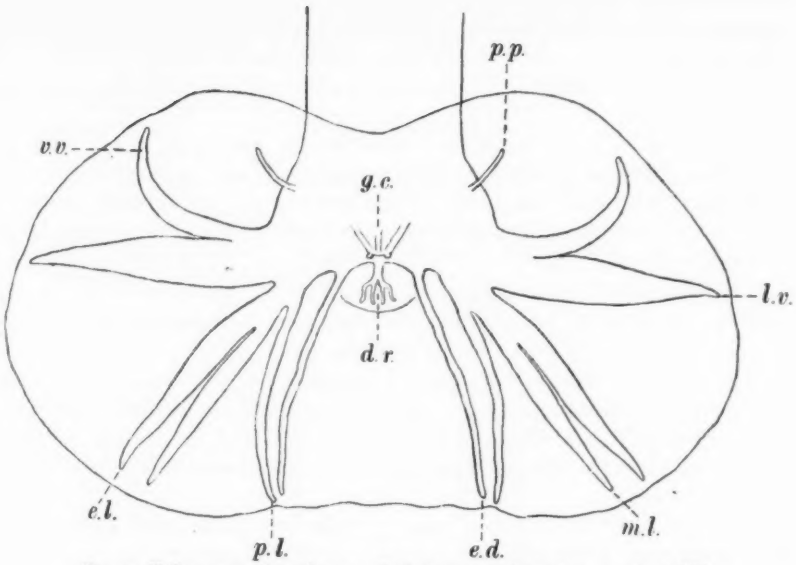


Fig. 3. *Heligmosomoides polygyrus.* Male bursa, ventral view. × about 350.

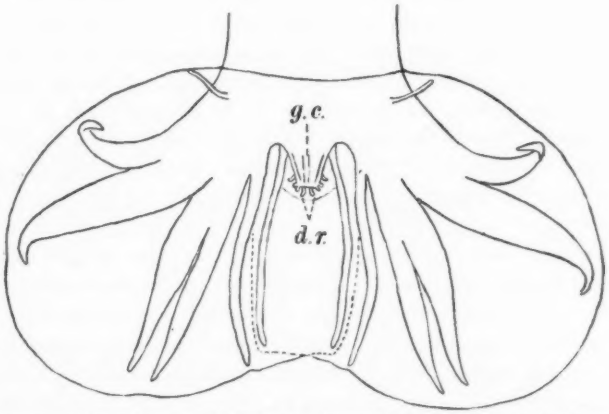


Fig. 4. *Heligmosomoides polygyrus.* Male bursa, incompletely spread out; the dorsal region is folded longitudinally so as to approximate the externo-dorsal rays, the genital cone covers the greater part of the dorsal ray. × about 350.

## EXPLANATION OF LETTERING.

*an.*, anus; *bu.*, buccal cavity; *cu.*, cuticular expansion of head; *d.r.*, dorsal ray; *e.d.*, externo-dorsal ray; *e.l.*, externo-lateral ray; *g.c.*, genital cone; *int.*, intestine; *l.v.*, latero-ventral ray; *m.l.*, medio-lateral ray; *oe.*, oesophagus; *p.l.*, postero-lateral ray; *p.p.*, prebursal papilla; *va.*, vagina; *v.v.*, ventro-ventral ray; *vu.*, vulva.

postero-lateral. The ventral rays arise from a common trunk and are markedly divergent; the latero-ventral is very thick, being quite twice as broad as the other bursal rays, the tip of the ventro-ventral ray is directed towards the anterior border of the bursa. Prebursal papillae are well developed and are long and slender.

The simple, filiform spicules are 0·5–0·58 mm. long, their distal portions are united. No gubernaculum could be traced.

**Female:** 6·2–10 mm. long. The greatest width of the body is in the posterior third, where it measures 0·09–0·12 mm.; the width in the middle of the body is 0·06–0·08 mm.

The anus is 0·067–0·1 mm. from the posterior extremity; the tail is conical, truncated posteriorly, and bearing a slender, pointed terminal spike which measures 0·012–0·018 mm. in length (text-fig. 1).

The vulva is a conspicuous opening, situated 0·24–0·35 mm. from the tip of the tail. The female organs are single; the ovejector is well developed and similar in shape to that described by von Linstow (1882), the combined length of the vagina and ovejector (exclusive of anterior nonmuscular portion) is 0·45–0·55 mm.

The eggs are 0·62–0·78 mm. long by 0·035–0·045 mm. wide, they are in the morula stage when laid.

The systematic position of *S. laevis* Dujardin remains to be considered. Stossich (1899) has suggested that this is a synonym of *S. polygyrus*. According to Dujardin the two worms are very closely allied and only to be distinguished with difficulty. He specially notes that the caudal extremity of the female is similar in the two species, *S. laevis* also having the extremity truncate and bearing a terminal spike. In the absence of any description of the male bursa we have only the female characters to help us in assigning a position to this worm among the genera of Heligmosominae; these strongly suggest that *S. laevis* should be placed alongside *S. polygyrus* in the genus *Heligmosomoides*.

Seurat (1915) has published a description of a worm from *Dipodillus campestris* in Algeria which he considers to be *S. laevis*; his account shows that in this form the bursa is divided into distinct dorsal and lateral lobes, and possesses a long dorsal ray, the branches of which extend to the bursal margin; the female tail is conical with a pointed termination. If these characters are correctly interpreted, I think there can be little doubt that Dujardin's species was not dealt with.

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# A PARASITIC COPEPOD BELONGING TO THE GENUS *MEDESICASTE* (KRØYER), AND ITS RELATION TO THE TUMOURS IT PRODUCES ON THE FISH, *TRIGLA GURNARDUS*.

By W. HAROLD LEIGH-SHARPE, M.Sc. (Lond.).

(With 7 Text-figures.)

**Habitat and record.** The genus *Medesicaste* (Krøyer), belonging to the family Chondracanthidae, is usually considered to be represented by but one British species, *Medesicaste asellinum* (Linn.)[1], whose characters are diagnosed as very variable. It is open to question whether the additional appendicular details given herein and the presence of the conjunctive tubes (*vide infra*) are sufficient to warrant the erection of a new species.

The following observations were made upon eight specimens of *Medesicaste* ♀ taken from various *Trigla gurnardus* caught at Lowestoft in August, 1918. They were, without exception, upon the gills, upon which they cause characteristic tumours.

**Body.** The outline of the animal is best seen from Figs. 1 and 2. The *cephalothorax* consists of a subglobose anterior end or head, bearing the antennules and antennae, and a considerably elongated slender neck at the base of which are situated the mouth and the other cephalic and thoracic appendages, which are thus widely separated from the antennae.

The *head* is 1·4 mm. long, bulbous, trilobate, rounded in front, with each side expanded into a hemispherical lobe. The *neck*, which has its posterior portion enlarged, is 1·8 mm. long. Both head and neck as far as the mouth are embedded in the tumour which is formed upon the gill-filaments of the host.

The *trunk* is square in outline, 2·4 mm. long, slightly wider than long. It is divided by a deep transverse constriction into two almost equal parts; the anterior constituting the thorax bearing appendages, carrying two pairs of obtuse processes ventrally and a small pair dorsally; the posterior, the larger, the genital segment, the antero-lateral corners of which extend outwards into angular projections. The lateral margins of this posterior division are arcuate, converging distally, and forming two small postero-lateral lobes between which is a small medio-ventral V-shaped depression or sinus.

[1] A full list of references and synonyms is given by Scott and Scott (1913). *The British Parasitic Copepoda*, The Ray Society, London. The only fairly good figure is that in this work, Plate LII, fig. 6.

The two ventral anterior thoracic processes curve ventrally and frequently meet. Each process bears a pair of pronounced, fleshy appendages, also curved, and always meeting, so that most specimens appear to have a fleshy loop at this point caused by the interlocking of the apical "digits."

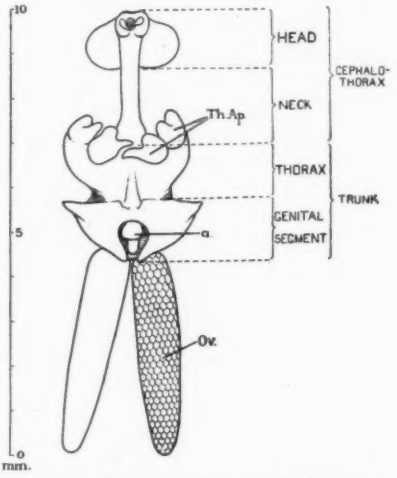


Fig. 1. *Medesicaste.* Ventral aspect. *a.* abdomen; *Ov.* ovisacs; *Th.Ap.* two pairs of ventral thoracic appendages.

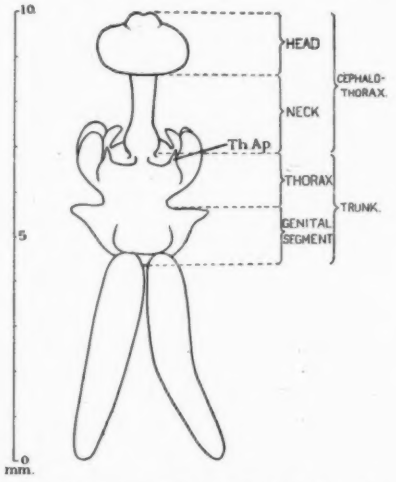


Fig. 2. *Medesicaste.* Dorsal aspect. *Th.Ap.* one pair of dorsal thoracic appendages.

The *abdomen* is very small, bi-articulated, the posterior segment being the larger, and enclosed between the postero-lateral lobes. There are no abdominal appendages.

The *ovisacs* are 4·4 mm. long, longer than the trunk, of a dark brown colour, and show externally six rows of ova, 31 in a row.

The total length of the preserved animal is about 10 mm. A fully developed female is found embedded in a relatively small tumour, has a larger trunk, bears two ovisacs, and has no trace of conjunctive tubes.

The **appendages,** all paired, none of them setigerous, are, in order, as follows (Fig. 3): The *antennules* are minute, two-jointed, the joints not making

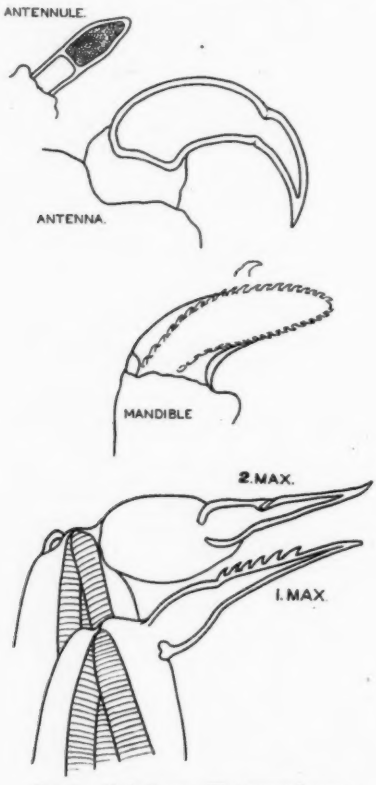


Fig. 3. *Medesicaste.* The appendages.

any angle with one another. The terminal joint is rounded. They are situated dorsally and are barely half the size of the antennae. The *antennae* (Figs. 3 and 4) are ventral, two-jointed, short and stout. The terminal joint, which is much the longer, terminates in a powerful, incurved, sharp-pointed claw. The *mandibles* are falciform as is usual in this family, instead of styliform as in the Lernaeopodidae, broad at the proximal end, and tapering to a more or less attenuated distal extremity. Both margins appear minutely serrated under a low magnification, but in reality the teeth, which resemble prickles,

are set at right angles to the undersurface of the lamina, and are marginal only at the apex, while they form a loop and do not approach the margin at the base. Towards the convex edge of the lamina the number of teeth is twenty; along the concave edge they are more numerous.

There follow two pairs of appendages of uncertain homology, variously styled *maxillae* or *maxillipedes*. They are both on the same plan, two-jointed, there being in each case a stout basal joint, with a bulbous distal joint, terminating in a long straight style. The anterior pair is distinguishable by having

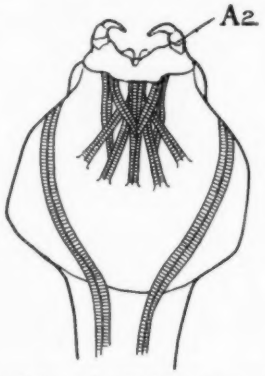


Fig. 4. *Medesicaste.* The anterior end, with the antennae (*A2*) in the erect position.

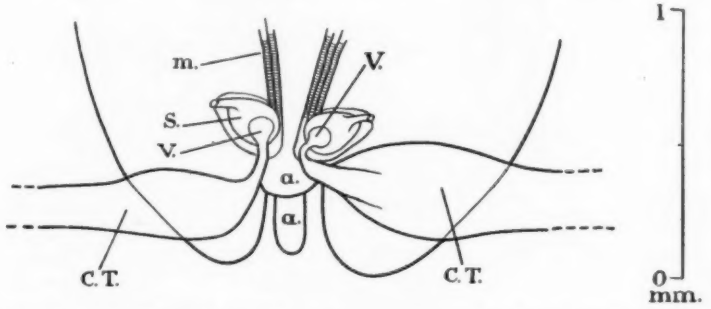


Fig. 5. *Medesicaste.* The posterior end. *a.* abdomen; *m.* muscle; *V.* vulvae; *S.* spermathecae; *C.T.* conjunctive tubes.

the inner margin of the style strongly serrated (Fig. 3, 1 *max.*). There are six large, stout spines away from the apex which interlock in a scissor-like manner with those of its partner. The *thoracic appendages* have already been described (*v. supra*); their surface is covered with numerous very minute prickles.

The most striking feature, now for the first time described, is the presence of the **conjunctive tubes.** These occur in three of the specimens, which are immature, bear no ovisacs and are embedded in relatively large tumours.

These tubes are paired, for although only one is preserved entire in each of the specimens, the broken end of the second is present in the best specimen (Fig. 6). The tubes are attached to the vulvae of the female and communicate directly with the spermathecae, the ovisacs issuing forth dorsally at another aperture. The reproductive system is on the same general plan as I have described for *Lernaeopoda* (*Parasitology*, VIII. 269 and Fig. 6), the ovaries occupying the arcuate lateral portions of the genital segment.

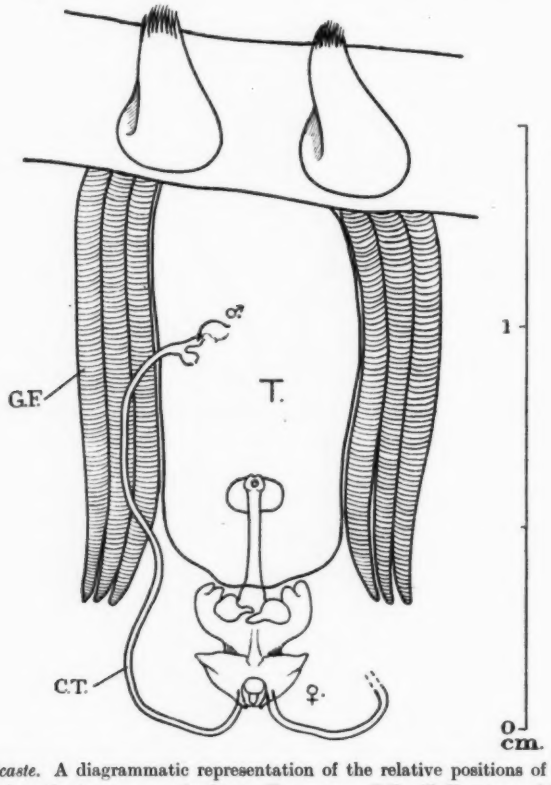


Fig. 6. *Medesicaste.* A diagrammatic representation of the relative positions of the two sexes with regard to the tumour on the host. *T.* tumour; *G.F.* gill filaments of host; ♀ female animal; ♂ male animal; *C.T.* conjunctive tubes.

A most remarkable phenomenon is that the other end of the tube, which is long, free, flexible and sinuous, enters the upper portion of the same tumour as that in which the head and neck of the female are embedded, where it bifurcates; hence the term "conjunctive" (Fig. 6). The tube is one third the width of a gill filament, and about 12 mm. long.

The tumour produced by the parasite is structureless and is to be regarded as a hypertrophied gill filament. It may be irregular, but is usually clavate,

with or without a constricted neck, about seven times the breadth of a normal gill filament. No doubt the hypertrophy was occasioned by the penetration of the free-swimming nauplius larva into the tissues of the gill filament.

At the proximal bifurcation of the conjunctive tube, deep within the tumour, are the faint traces of what appear to be the remains of the cuticle of a dead and disintegrated male, the only certain detail of which is the rounded dorsum (Fig. 7). If this be proved, the tubes might be definitely called conjugation tubes, exhibiting an occurrence wholly unique. During the past four years I have examined some hundreds of gurnards without finding *Medesicaste*, neither has that genus been taken at the laboratory of the Marine Biological Association, Plymouth, though specially sought at my request.

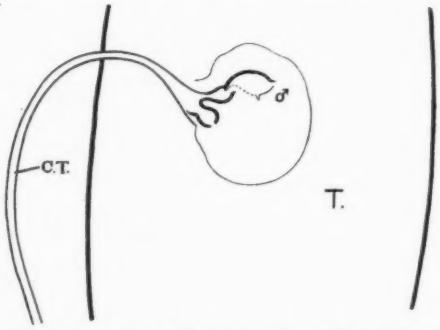


Fig. 7. *Medesicaste*. An enlarged view of the entrance and bifurcation of a conjunctive tube (*C.T.*) in the tumour (*T*). ♂ remains of male animal.

## SUMMARY.

A tumour among the gill filaments of *Trigla gurnardus* bears a female *Medesicaste* with the head and neck buried in its apex, and a male *Medesicaste* completely embedded in its base. The two sexes of the parasite are connected by a conjugation tube, *external* to the tumour, down which tube the spermatophores presumably pass. The appendages of the copepod are described.

My thanks are due to Michael G. L. Perkins for furnishing me with the specimens, and to Miss Edith C. Humphreys for drawings of the specimens and preparations which are all mounted unstained in Farrant's medium.

# PARASITISM AND SYMBIOSIS.

## (A REVIEW.)

PARASITOLOGY, owing to its economic importance, has received very great attention during the last 50 years and several good text-books have been devoted to this subject. In almost all recently published books, however, stress has been laid chiefly upon the economic side of the problem: medical, veterinary, agricultural, etc., but the scope of Parasitology is by no means restricted to the problems economically connected with man. We know now that there is hardly any group in the animal or vegetable kingdom which does not harbour parasites. The latter themselves do not escape this rule and are often parasitised in their turn. Moreover, the interrelations between living organisms are not restricted to parasitism only; there are, in fact, all shades of transition between parasitism on the one hand, and commensalism and symbiosis on the other. These interrelations have never been adequately dealt with in text-books of biology or parasitology and all the information concerning them is scattered in a great number of papers dealing with various biological or parasitological problems. This gap has been recently filled by a small volume issued by Prof. M. Caullery [of the "Laboratoire d'Evolution des Êtres Organisés de la Sorbonne, Paris] under the title *Le Parasitisme et la Symbiose*[1] in which the author has incorporated a series of lectures delivered by him on this subject during the academic year 1919–1920. The book deals with the most interesting cases of commensalism, parasitism, and symbiosis and with various important cases of transition between these three great ethological groups.

In discussing parasitic adaptation, the author has examined not only the classical cases of parasitism found in the text-books, but he has also included many interesting examples of other parasitic groups such as Crustacea, Polychaeta and especially Mollusca which show a remarkable series of transitions between ecto- and endo-parasitic life. The author summarises also the results of investigations on several helminths, *i.e. Schistosoma, Dibothriocephalus* and *Ascaris*, whose life-histories have been successfully worked out during the last few years.

Special prominence is given to a series of problems of general parasitology: (1) parasitic adaptations, (2) the influence of the parasite upon the host, especially parasitic castration, (3) reaction of the host (phagocytic reaction and elaboration of antiferments, formation of galls, etc.). The last part of the book deals with symbiosis. In the chapters discussing symbiosis in plants, the author lays special stress on the very important work of Noël Bernard upon the symbiosis existing between the Orchidae and Fungi. In dealing with symbiosis in animals, apart from classical examples, attention is given to symbiosis between Insects and yeasts and the intracellular symbionts in Cephalopoda. Portier's views on the dualism of a living cell and the relation between the symbionts and mitochondria are submitted to a searching criticism. Prof. Caullery concludes that there is complete lack of evidence in support of this theory as we know now that mitochondria are characterised by a very low resistence while the symbionts cultivated by Portier appear to be highly resistant. The author finally refers to recent work on the aseptic breeding of various animals, and especially Insects. This short review only faintly indicates the various problems of general parasitology dealt with by the author.

The book will serve as a well of information for teachers who will find in it ample illustrations of all kinds of interrelations between living organisms; it should stimulate original research and enable workers in different fields of parasitology to coordinate the results of their investigation with those already obtained and generalised in this most interesting volume.

D. KEILIN.

[1] Caullery, M. (1922). *Le Parasitisme et la Symbiose*. Encyclopédie scientifique. Librairie Octave Doin. Editeur Gaston Doin, 8 Place de l'Odéon, Paris. 400 pp. + 51 figs. Small in 8°.